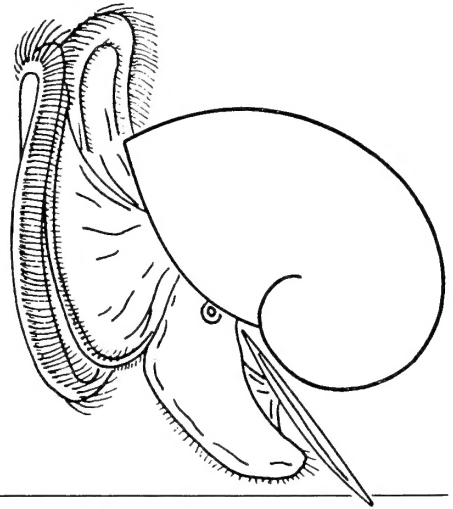


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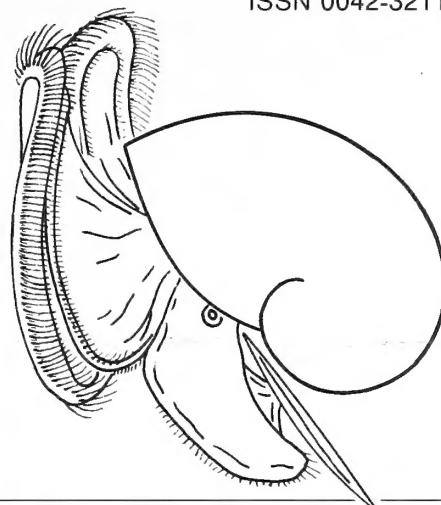
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THE VELIGER

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This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, evolutionary, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Systematic Position of Three European Heterobranch Gastropods

by

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Abstract. The external morphology of the soft parts, the shell, and the radula are described for the two Mediterranean gastropod species *Oxystele depressa* Granata (formerly in the Skeneidae) and *Skenea pellucida* Monterosato (formerly in the Skeneopsidae). *Oxystele depressa* is transferred to *Tomura* Pilsbry & McGinty, 1946 (Cornirostridae). *Skenea pellucida* is made the type of *Xenoskenea* Warén & Gofas, gen. nov., and classified in the family Hyalogyrinidae, a heterobranch family with rhipidoglossate radula. *Noerrevangia fragilis* Warén & Schander, gen. et sp. nov. (Cornirostridae) is described from shallow water around the Faeroe Islands.

INTRODUCTION

Small, globular or low spired, "skeneimorph" and "vitri-nellid-like" gastropods have for many years presented great problems for authors trying to classify them (Mediterranean species reviewed by GHISOTTI, 1984). The species have frequently been transferred between genera like *Skenea*, *Daronia*, *Cyclostrema*, *Skeneopsis*, *Tubiola*, *Vitrinella*, *Teinostoma*, and others. WARÉN (1992) attempted to stabilize the classification of some of the European species, mainly those belonging to the "Archaeogastropoda." This paper deals with three additional species belonging to the Heterobranchia.

Examination of living specimens of *Oxystele depressa* Granata and *Skenea pellucida* Monterosato showed that these species cannot belong to the families or genera where they previously were classified (Skeneidae and Skeneopsidae; SABELLI *et al.*, 1990), but have to be classified in two recently established families, Cornirostridae Ponder, 1990b, and Hyalogyrinidae Warén & Bouchet, 1992.

Noerrevangia fragilis gen. et sp. nov. (described herein) was found by Schander during field work at the Faeroe Islands. From the external morphology of the soft parts and from radular morphology this species fits well in the Cornirostridae.

The Cornirostridae and Hyalogyrinidae, in which these species are included, are not very well known to most malacologists, and the Heterobranchia, where they are classified, has been considerably enlarged during the last three years by the addition of a number of new families (listed herein, see "Systematics"). We therefore give a short supplement to the discussion by PONDER (1991) on this group.

MATERIALS AND METHODS

This paper is partly based on observations made on live specimens of *Oxystele depressa* and *Skenea pellucida* during field work. Color drawings were prepared and notes were based on weakly anesthetized specimens observed under a

stereomicroscope with a drawing tube. The observations are supplemented by the examination of shells from various collections. *Noerrevangia fragilis* was obtained in sediment residues fixed in formalin during field work in the Faeroe Islands, and it was not possible to examine the specimen alive. The soft parts were therefore extracted, stained with carm-alum, and examined under a stereomicroscope. Afterwards they were critical point dried and examined with scanning microscopy. Subsequently the soft parts were rehydrated and the radula extracted by dissolving the tissues in KOH.

The material we have had access to is listed under each species, with the location of the material: BMNH—Natural History Museum, London; MNHN—Muséum National d'Histoire Naturelle, Paris; SMNH—Swedish Museum of Natural History, Stockholm; USNM—United States National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Subclass Heterobranchia

PONDER (1991) discussed the following superfamilies and families as being of importance for the understanding of early heterobranch phylogeny:

- Valvatoidea: Valvatidae, Orbitestellidae, Cornirostridae (see PONDER, 1990a, b, 1991; HEALY, 1990)
- Architectonicoidea: Architectonicidae, Mathilididae
- Pyramidelloidea: Pyramidellidae, Amathinidae
- Omalogyroidea: Omalogyridae
- Rissoelloidea: Rissoellidae
- Glacidorboidea: Glacidorbidae (PONDER, 1986).

Four families have afterwards been added to the early heterobranchs:

- Provalvatidae Bandel, 1991 (Valvatoidea; fossil, Jurassic)
- Hyalogyrinidae Warén & Bouchet, 1992 (superfamily uncertain)
- Tjaernoidea Warén, 1991 (superfamily uncertain)
- Xylodisculidae Warén, 1992 (superfamily uncertain).

New heterobranch families based on the genera *Ebala* Gray, 1847 (Pyramidelloidea) and *Cima* Chaster, 1897 (unknown superfamily) are in the process of being described (Warén, unpublished).

PONDER & WARÉN (1988) and PONDER (1991) favored an opinion that the Heterobranchia and Caenogastropoda were independently derived from different "archaeogastropod" groups and that the archiotaenioglossates represent an early offshoot of the branch leading to the caenogastropods. The recognition of the family Hyalogyrinidae (WARÉN & BOUCHET, 1992), with many heterobranch characters (Haszprunar, in preparation) and a rhipidoglossate radula strongly supports Ponder's view, rather than the scenario proposed by HASZPRUNAR (1988), who considered the heterobranchs and caenogastropods to be

derived from a common ancestor, above the archaeogastropod level.

The detailed relations between the families listed above and the "subclasses" Pulmonata and Opisthobranchia are still incompletely known.

At present the most important task for increasing the knowledge about the lower heterobranchs is to extract, from the muddle of small "archaeo-" and caenogastropods, the right candidates for further exploration of the "missing links" between, on one side the "archaeo-" and caenogastropods, and on the other side between the "archaeogastropods" and the heterobranchs.

Family CORNIROSTRIDAE Ponder, 1990

Remarks: The family Cornirostridae was erected by PONDER (1990b) for the genera *Cornirostra* and *Tomura*, which are characterized by the following synapomorphies (in addition to a number of anatomical characters, which have not been examined in the species discussed herein and therefore cannot be evaluated):

- a bifurcate snout
- an anteriorly bifurcate foot
- a posteriorly bifurcate foot
- a single right pallial tentacle
- a bipectinate, basally attached ctenidium
- a hermaphroditic reproductive system with cephalic penis
- production of gelatinous egg masses
- a central radular tooth with highly developed lateral supports
- two or three partly overlapping lateral teeth.

The species of Cornirostridae are astonishingly similar to species of Vitrinellidae in their shell characters. Some species, for example *Tomura depressa*, can be recognized as belonging to the Heterobranchia by their heterostrophic larval shell, but an examination of the radula is usually needed to confirm the familial position.

Ponder interpreted the radula of *Cornirostra* to be taenioglossate, but we consider PONDER's (1990b:534, 543) "accessory plate" to be a third lateral tooth (PONDER, 1990b:figs. 4A, E).

In the same way it can be seen from PONDER's (1990b) fig. 3A of *Tomura bicaudata* Pilsbry & McGinty, that each row consists of nine teeth. The two lateral teeth are stuck together, but in fig. 3D, the outer lateral tooth has been bent towards the marginal tooth (to the right). In our Figure 9 this is more obvious, since the serrated lateral margin of the inner lateral tooth can be distinguished.

We therefore assume that *Cornirostra* and *Tomura bicaudata* have nine teeth per transverse row. Ponder (personal communication) has agreed with this interpretation.

It can also be seen from PONDER's (1990b) fig. 4D and E of *Cornirostra* that it is only the most lateral tooth which folds laterally when the radula is "opened." This is also our experience from *Tomura depressa* (Figures 7, 10). (In

T. bicaudata the two outer teeth fold laterally.) In a taenioglossate radula this unfolding takes place between the second and third tooth, and the two marginal teeth will be folded laterally. Consequently the radular formula of *Cornirostra* should be 1·3·1·3·1 and that of *Tomura* (*bicaudata*) 2·2·1·2·2 or (*depressa*) 1·2·1·2·1.

In the Orbitestellidae the transverse rows of teeth consist of five teeth (PONDER, 1990a). We can therefore not agree that these radulae are taenioglossate. This does not, however, disturb the relations between the Cornirostridae and the Valvatidae, because the presence of a rhipidoglossate radula in *Xenoskenaea*, *Hyalogyra*, and *Hyalogyrina* suggests the presence of such a radula in the early heterobranchs and that the taenioglossate condition of the valvate radula is not homologous to that of the Caenogastropoda, although the radulae have the same number of teeth.

Noerrevangia fragilis also has the formula 2·2·1·2·2. Such a radula, as well as that of *Cornirostra* and *Tomura*, may have evolved from a rhipidoglossate-like radula similar to that of the Hyalogyrinidae.

Tomura Pilsbry & McGinty, 1946

Tomura PILSBRY & MCGINTY, 1946:15. Type species, by monotypy *Virtrinella* (*Tomura*) *bicaudata* Pilsbry & McGinty, 1946 (Florida).

Remarks: The crawling animal and the shell of the type species were figured by PILSBRY & MCGINTY (1945:pl. 2, fig. 9) and described in some detail by PONDER (1990b), based on topotypic material.

Tomura depressa differs from the type species in having one tooth less in the marginal field and by having a shell with an umbilicus. This will probably turn out to be of generic value, but since at present these two species are more similar to each other than to any other known species, we prefer not to introduce additional generic names before we can see a need for it.

Tomura depressa (Granata, 1877)

(Figures 1–11)

Oxystele depressa GRANATA, 1877a:146; GRANATA, 1877b:9.
Tharsiella tinostomoides FEKIH & GOUGEROT, 1977:224.

Type material: *Oxystele depressa*, not known; *Tharsiella tinostomoides*, holotype and 1 paratype from the type locality, 5 paratypes from Tunisia, Porto Farina, in MNHN.

Type localities: *Oxystele depressa*, Sicily, Strait of Messina, 65 m; *Tharsiella tinostomoides*, Gulf of Tunis, Khéredinne.

Material examined: TUNISIA: Golfe de Gabès: NW of Mer de Bou Grara, diving, 10–15 m, 150 shells (MNHN); Canal d'Ajim, diving 10–32 m, 10 shells, 2 specimens (SMNH); Djerba, SE of El Kantara, 4–5 m, 3 shells (MNHN); Sfax, 3 shells, *leg.* Gougerot (MNHN); Gulf of Tunis, Porto Farina, 20 shells, *leg.* Gougerot (MNHN).

FRANCE: Corsica, Baie de Calvi, algal washing, 10–40 m, 2 shells (SMNH); Marseille, off Mejean, 37 m, 2 shells (MNHN).

ITALY: Livorno, off Capraia, 180 m, coll. F. Giusti, 1 shell; Sicily, Catania, Acitrezza, shell gravel, 36 m, 3 shells (SMNH); Sicily, Bay of Brucoli, 17 m, 1 specimen (MNHN).

SPAIN: Málaga, dredged in 20–40 m, 2 shells (MNHN).

Distribution: Throughout the Mediterranean and Rabat (Atlantic Morocco), usually in 10–50 m (OLIVERIO, 1982, 1985, 1988; our material). Shells commonly found, live-taken specimens rare.

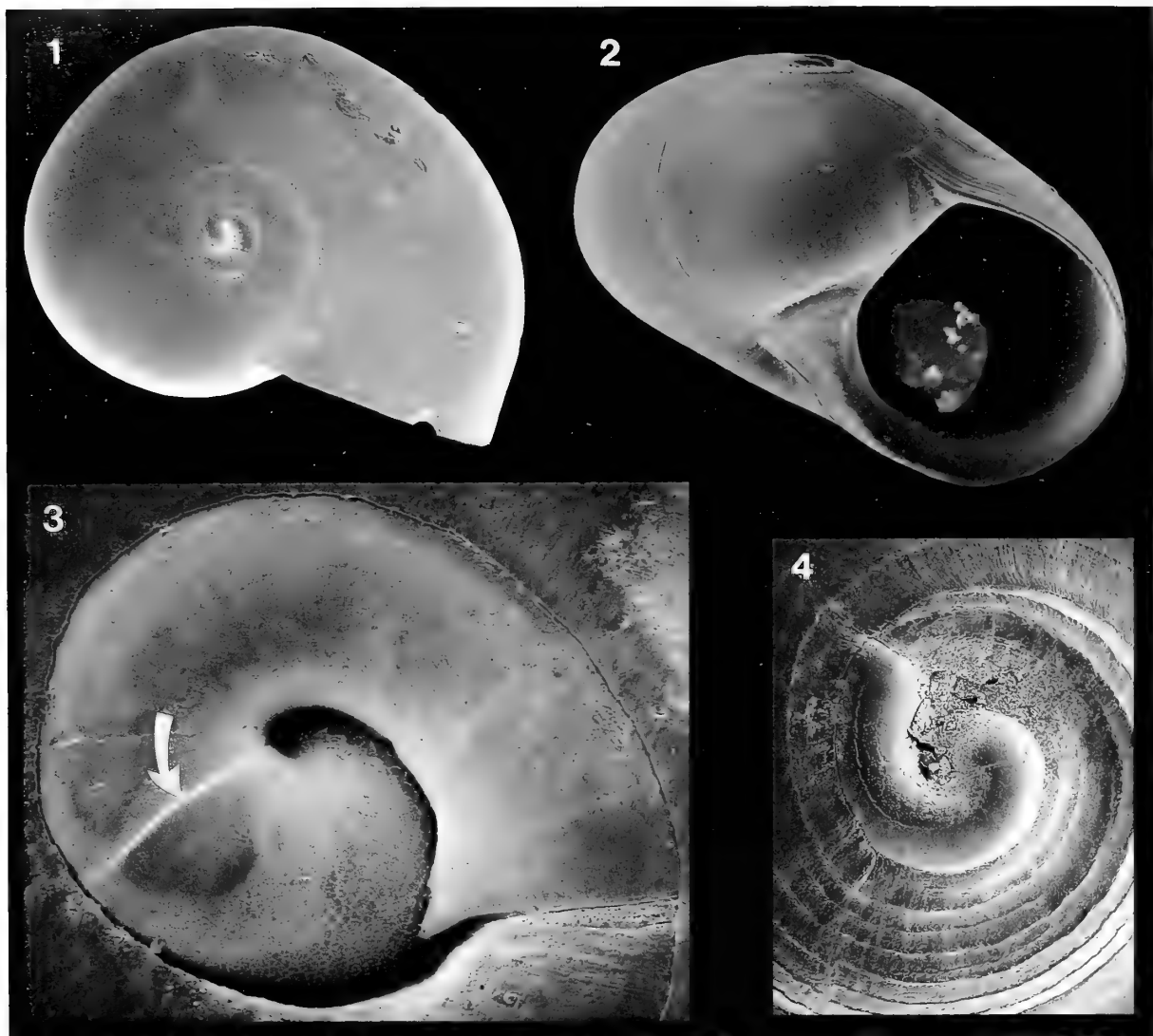
Redescription: The shell (Figures 1, 2) is very small, *Natica*-like, with an umbilical callus, transparent and rather solid. The larval shell (Figure 3) is hyperstrophic, diameter 150–175 µm. Protoconch I is only partly visible, and is mainly sculptured by a system of branching and anastomosing small ridges, except close to the demarcation to protoconch II. Protoconch II is almost smooth with only a few incremental lines and spirally arranged granulae, and consists of about 0.7 whorl. The teleoconch consists of about 2.0 whorls, usually almost perfectly smooth, separated by a very indistinct and shallow suture. Occasional specimens differ in having the initial part of the teleoconch equipped with a few spiral ridges (Figure 4), but this character varies in strength. The aperture is prosocline, almost tangential with the inner lip spread out to form a solid parietal and umbilical callus.

Dimensions: Maximum diameter 1.6 mm.

Operculum (Figure 11): It is thin and transparent, multispiral with short growth zone and central nucleus.

Radula (Figures 7–10): Formula 1·2·1·2·1. The radula is rather short and broad with about 20 transverse rows. The marginal tooth is broad and flat, roughly rectangular, with the distal end slightly obliquely truncated and denticulate. The outer, distal corner is slightly drawn out and cusplike, and the outer side of the tooth is finely denticulate almost to its base. The outer lateral tooth is short, rounded with the inner corner somewhat drawn out. This tooth is denticulate along its outer and apical sides. The inner lateral tooth is broad, apically evenly rounded and finely denticulate all around. The central tooth has a pair of lateral, wing-shaped supports and a central, distinct supporting ridge. The triangular cutting edge is serrated with about 9–11 denticles on each side of a central cusp. When tilted backwards, the distinctive anterior furrow becomes more obvious.

Soft parts (Figures 5, 6): The animal is almost colorless except for the pale brownish digestive gland and milky white cells in the anterior pedal gland. A small, bright yellow pigmented mantle organ is visible, dorsally and immediately behind the gill, through the shell. The foot is large, broad, thin, anteriorly expanded with drawn-out corners and is shallowly bifurcate; the sides are otherwise parallel; posteriorly it has a deep U-shaped notch, giving the posterior end a bifid appearance. The propodium is



Explanation of Figures 1 to 4

Figures 1–4. *Tomura depressa*, Canal d'Ajim, between Djerba and mainland, Tunisia. Figure 1. Apical view, 1.25 mm. Figure 2. Front view, 1.36 mm. Figure 3. Larval shell, diameter 171 μ m. The arrow indicates the demarcation of protoconch I and II. Figure 4. Unusually strongly sculptured specimen, diameter of larval shell 152 μ m.

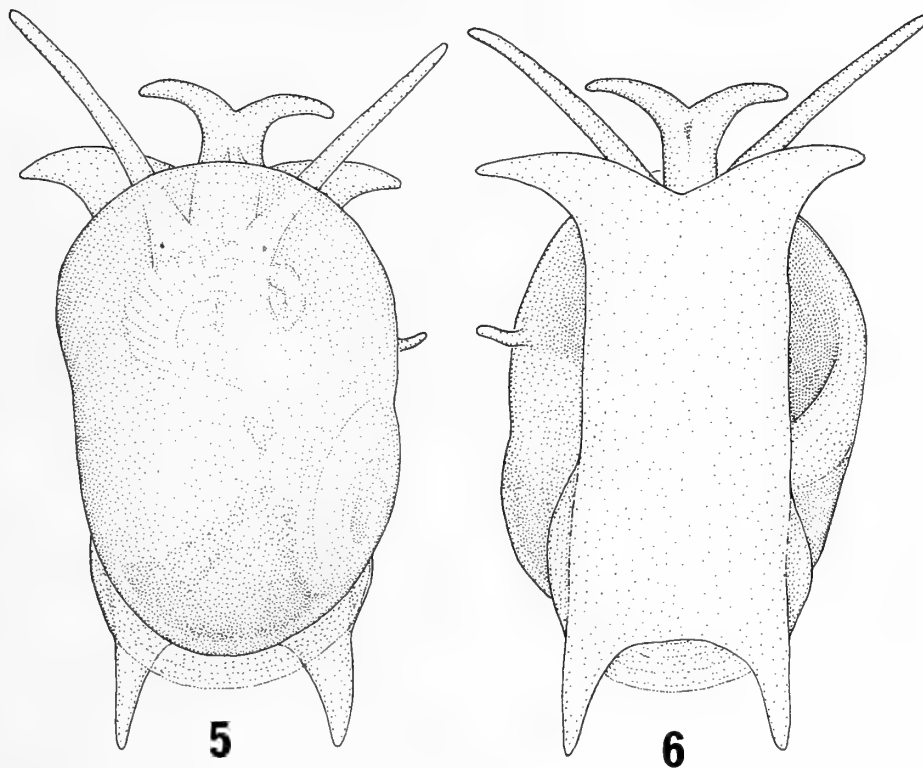
not demarcated from the mesopodium; the metapodium (opercular lobe) forms a thin fold between the operculum and the mesopodium, hanging free between the two "tails." The head is small and slender, with long, cylindrical tentacles; the eyes are very small and deeply buried in the tentacle bases. A small, elongate, slightly tapering penis is attached laterally just to the right of the right cephalic tentacle. The snout is long and cylindrical, distally deeply bifurcate; a pair of jaws can be seen through the transparent central part of the snout. A minute pallial tentacle is present at the right corner of the pallial margin. The ctenidium is triangular, bipectinate, and attached basally.

Remarks: OLIVERIO (1982, 1985, 1988) reviewed the Mediterranean species *Tharsiella romettensis* (Granata) and

T. depressa (Granata), their nomenclatorial history, and their distribution, but kept them both in *Tharsiella*, classified in the Skeneidae. For comments on *Tharsiella*, which is a junior synonym of *Cirsonella* Angas, 1877 (provisionally in Skeneidae) and *T. romettensis*, see WARÉN (1992).

Our description of the soft parts is based on two specimens observed alive. One, examined in the Golfe de Gabes, Tunisia, was taken on a sandy bottom in Canal d'Ajim, between Jerba and the mainland. The second specimen was taken on a sandy bottom off Brucoli in eastern Sicily, at 17 m depth. The rarity of live specimens is probably because the precise habitat is still unknown.

The external morphology of the head-foot of *Tomura depressa* agrees well with that of the type species of *Tomura* (cf. Figures 5, 6 with PONDER 1990b:fig. 2), but the shell



Explanation of Figures 5 and 6

Figures 5, 6. *Tomura depressa*, crawling animal. Sicily, off Brucoli, 17 m depth. Penis, jaws, eyes, and ctenidium visible through transparent tissues.

differs from *T. bicaudata* in lacking the umbilicus, which in *T. depressa* is filled out by a callus. PONDER (1990b) did not, however, find a pigmented mantle organ in *T. bicaudata* and the pallial tentacle is shorter in *T. depressa*.

The shell of *Tomura depressa* has the appearance of a miniaturized *Natica* with an umbilical callus, but examination of the larva shell shows that the initial whorl is very small, tilted, and depressed. Furthermore, the diameter of the protoconch is less than 0.2 mm, whereas the larval shell of European species of Naticidae with an umbilical callus has a diameter of about 1 mm or larger—i.e., comparable to the size of an adult *T. depressa*.

Noerrevangia Warén & Schander, gen. nov.

Type species: *Noerrevangia fragilis* Warén & Schander, sp. nov.

Diagnosis: Small, *Vitrinella*-like cornirostrids with a paucispiral protoconch of half a whorl, and radular formula 2·2·1·2·2. Penis exceptionally large, equipped with open seminal gutter (Figure 19).

Description: See specific description of *Noerrevangia fragilis*.

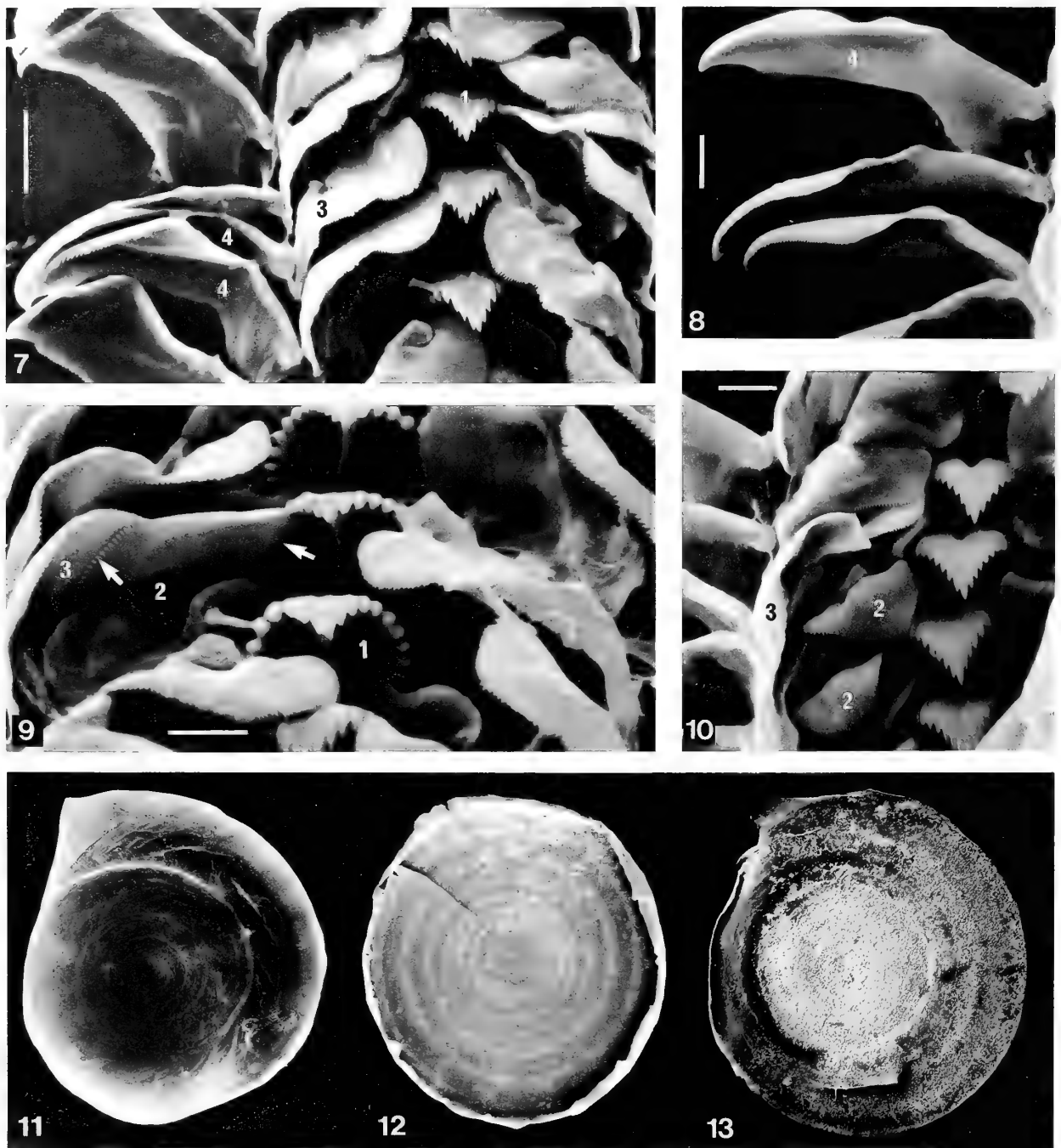
Etymology: Named after Professor Arne Nørrevang, director of the Kaldbak Marine Laboratory at the Faeroe Islands.

Remarks: The systematic position of *Noerrevangia* is not obvious from the shell. The anteriorly and posteriorly divided foot, the bifurcate snout, and the radular morphology do, however, indicate relations with the Cornirostridae. Additional similarities, although less diagnostic, are the right pallial tentacle, the presence of a cephalic penis, the bipectinate ctenidium, and the shape of the shell.

The shell and the head-foot of *Noerrevangia* closely resemble those of *Cornirostra*, but the spire of *Noerrevangia* is much more depressed and the penis of *Noerrevangia* has an open seminal gutter (internal in *Cornirostra*). We have therefore introduced a new genus.

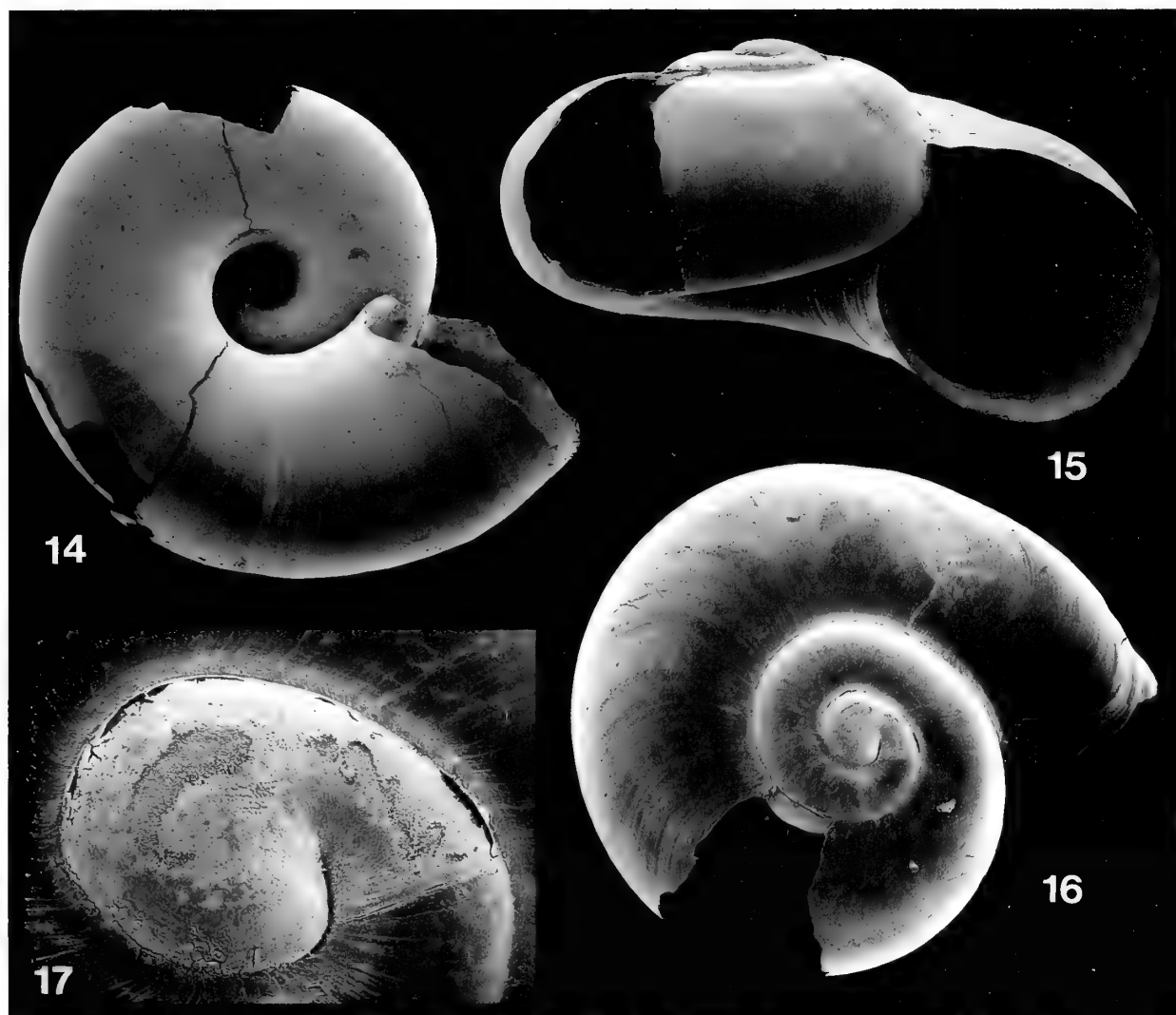
The radulae of *Tomura* and *Cornirostra* differ from that of *Noerrevangia* in the number of the marginal teeth (two in *Noerrevangia*, one or two in *Tomura*, and one in *Cornirostra*), the number of lateral teeth (two in *Noerrevangia*, three in *Cornirostra*, two in *Tomura*), and the shape of the inner lateral tooth, which has two main cusps in *Noerrevangia*. (The two cusps of the first lateral tooth of *N. fragilis* may, however, be the result of fusion of two teeth.) The central tooth of the three genera shows great similarity in the development of the winglike lateral processes.

The protoconch of *Noerrevangia* is not similar to that of the other cornirostrids, but since there is no trace of a protoconch II, the development can be assumed to be lecithotrophic. In connection with a change from plankto-



Explanation of Figures 7 to 13

Figures 7-13. Radulae and opercula. Figures 7-11. *Tomura depressa*, Canal d'Ajim, between Djerba and the mainland, Tunisia. Arrows indicate indistinct borders between teeth; numbers indicate the sequence of the teeth, with the central tooth as number one. Figure 7. Vertical view. Scale line 10 μ m. Figure 8. Another view of marginal teeth. Scale line 10 μ m. Figure 9. Posterior view of central and lateral teeth. Scale line 5 μ m. Figure 10. Vertical view of another specimen. Scale line 5 μ m. Figure 11. Operculum, diameter 0.88 mm. Figures 12, 13. *Xenoskenea pellucida*, operculum, Sicily, diameters 0.46 mm and 0.91 mm.



Explanation of Figures 14 to 17

Figures 14–17. *Noerrevangia fragilis* gen. et sp. nov., holotype. Figures 14–16. Shell, diameter 1.7 mm. Figure 17. Larval shell diameter 270 μ m.

trophic development to lecithotrophic, great changes in the shape of the protoconch are common and we consider this difference of minor importance.

Although seemingly a minor detail, the fact that the penis is lying parallel to the cephalic tentacle may signify an important character. Almost all caenogastropods keep the penis folded backwards, so it lies along the right corner of the pallial cavity. The position may, however, also be a preservation artifact.

Noerrevangia fragilis
Warén & Schander, sp. nov.

(Figures 14–25)

Type material: Holotype (now badly broken) SMNH 4423.

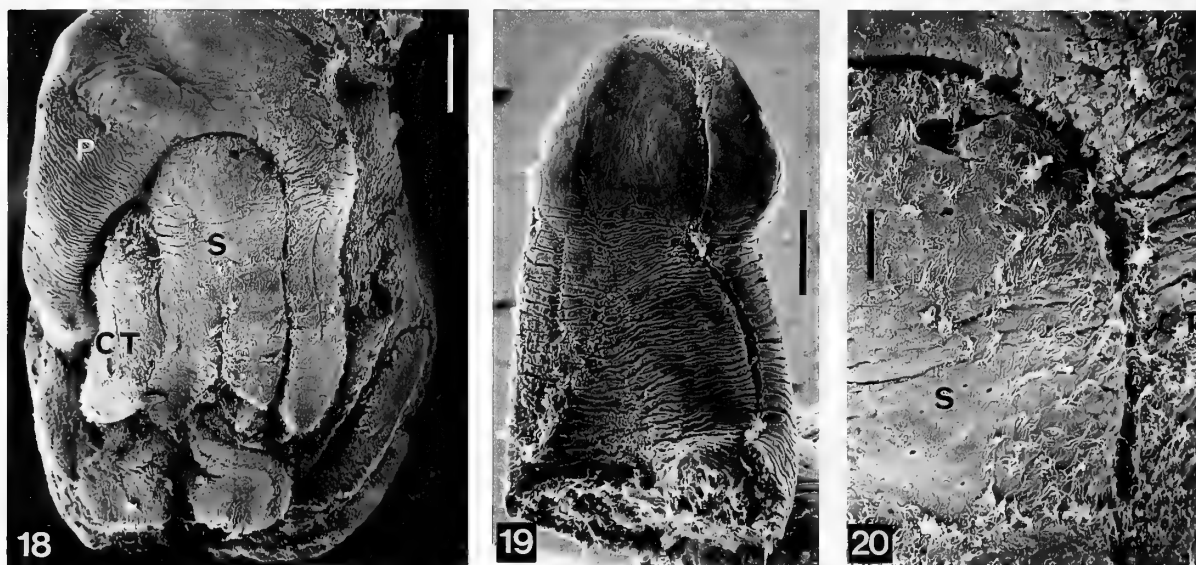
Type locality: The Faeroe Islands, off Thorshavn, 62°04.5'N, 06°42.8'W, 43 m, clay bottom.

Material examined: Known only from the holotype.

Distribution: Known only from the type locality at the Faeroe Islands, in 43 m depth.

Etymology: *Fragilis* (Latin), meaning “fragile.”

Description: The shell (Figures 14–16) is small, transparent, vitrinellid-like with a depressed spire, and is very fragile. The larval shell (Figure 17) consists of slightly more than half a whorl with a diameter of 270 μ m. It is low and depressed in shape and there are traces of a finely granular sculpture on the initial part, but this area is slightly corroded in the unique specimen. The teleoconch consists of 2.0 whorls of a rounded cross section, slightly



Explanation of Figures 18 to 20

Figures 18–20. *Noerrevangia fragilis* gen. et sp. nov., holotype, critical point dried. Figure 18. Contracted head-foot, anterior view. Scale line 100 μm . Figure 19. Penis, ventral view, showing the seminal furrow. Scale line 50 μm . Figure 20. Snout and cephalic tentacle, surface structure. Scale line 25 μm . Key: CT, cephalic tentacle; P, penis; S, snout.

indented by the preceding whorl. The sculpture consists of rather indistinct and slightly flexuous incremental lines. The suture is distinct but not depressed since the outer lip makes a distinct adapical deviation from its circular shape, evening out the transition to the preceding whorl. The aperture is distinctly prosocline and the outer lip slightly sinuated just below the suture. The umbilicus is broad and deep and penetrates the shell to the protoconch.

Dimensions: Diameter 1.7 mm.

Operculum: Round, stiff, colorless, multispiral and smooth, with central nucleus.

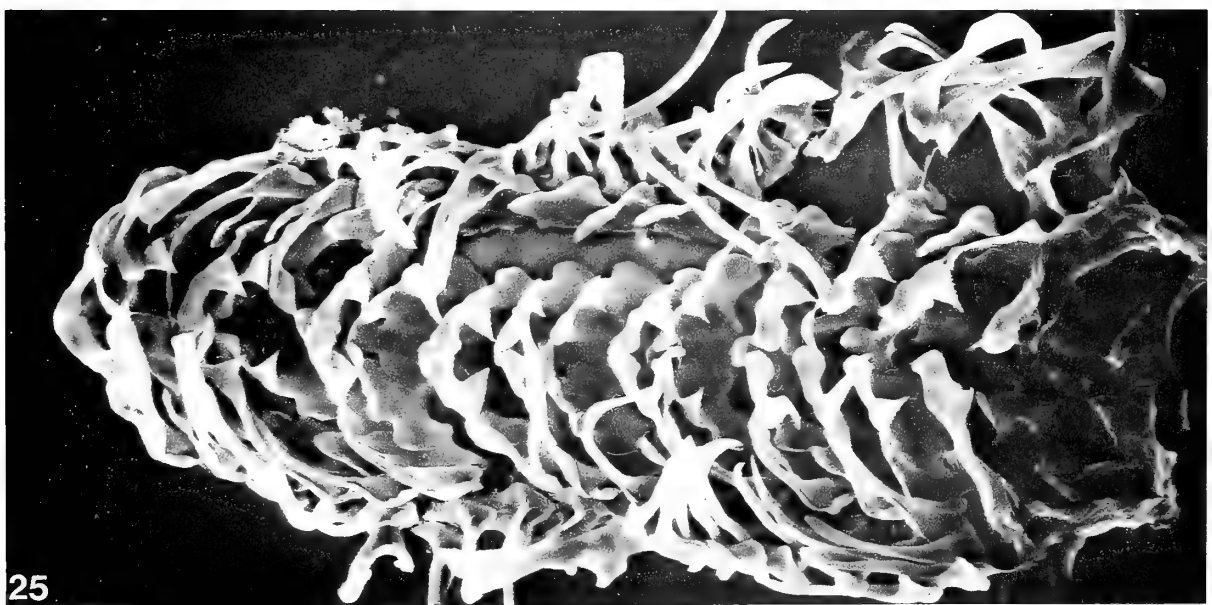
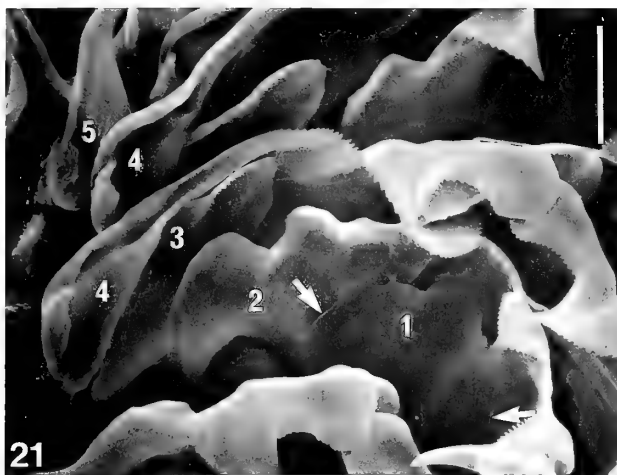
Radula (Figures 21–25): Formula 2·2·1·2·2. Central tooth with a sturdy, pointed, and serrated cutting edge and winglike basal supporting ridges. The first lateral tooth is very broad and has two cutting plates, one rounded and more central and one more pointed at the midpoint of the tooth. Lateral to this cutting plate the tooth has a winglike lateral protrusion. The second lateral tooth is very broad and has a rounded, serrated cutting plate occupying the inner one-third of the apical margin. The two marginal

teeth are oarlike, long, slender, and serrated along the apical one-third, where they have a thin web along the edge.

Soft parts (Figures 18–20): The foot is anteriorly deeply divided and the corners are drawn out laterally. The propodium is narrow and inconspicuous. Posteriorly the foot does not taper regularly to a point, but probably is deeply notched, as in *Tomura* (but should could not be ascertained because of the contraction of the preserved animal). No epipodial ridges or tentacles were noticed. The snout is long, slender, and bifurcate to half its length. The cephalic tentacles are only sparsely ciliated, are slightly longer than the snout, and lack sensory papillae. Pigmented eyes are lacking. The large penis, attached just behind the right cephalic tentacle, is twice as broad and slightly longer than the tentacle. Its anterior, ventral edge has a deep seminal groove (Figure 19) that lies along the cephalic tentacle. The pallial edge is smooth and simple. Its right corner has a richly ciliated pallial tentacle of half the length of the cephalic tentacles. The ctenidium, which is large and bi-

Explanation of Figures 21 to 25

Figures 21–25. *Noerrevangia fragilis* gen. et sp. nov., radula of the holotype. Numbers indicate the sequence of the teeth, with the central tooth as number 1. Arrows indicate borders between teeth. Figure 21. Oblique view of central and lateral teeth. A marginal tooth (4) is concealing the outer part of the outer lateral tooth. Scale line 10 μm . Figure 22. Oblique view of central and lateral teeth. The point of the more anterior central tooth (1) is concealed by a marginal tooth. Scale line 5 μm . Figure 23. Oblique view of central and lateral teeth. Lateral “wing” of central tooth broken. Scale line 5 μm . Figure 24. Oblique view of lateral teeth. Slightly different angle of Figure 21. Scale line 5 μm . Figure 25. Complete radula, length 215 μm .



pectinate, occupies two-thirds of the width of the pallial cavity in the holotype. The digestive gland is richly spotted with brown granules.

Remarks: The shell of this new species is featureless and it would presently be impossible to classify it from conchological characters only. Among European genera it resembles *Skeneopsis* (Skeneopsidae), but species of that genus have a reddish or brownish, more solid shell with a deeper suture, and a protoconch of slightly more than one whorl sculptured with spiral lines and granules. We illustrate the shell, protoconch, and radula of the type species for comparison (Figures 37–41).

The more archaeogastropod-like genus *Akritogyra* Warén, 1992 (systematic position uncertain, provisionally in Skeneidae), resembles *Cornirostra* and *Noerrevangia*, but the shell has a slightly taller spire and the species have a rhipidoglossate radula with the formula $4-6 \cdot 2 \cdot 1 \cdot 2 \cdot 4-6$ (WARÉN, 1992). The soft parts of *Akritogyra* are still poorly known.

Family HYALOGRYNIDAE Warén & Bouchet, 1992

Two genera (*Hyalogyra* and *Hyalogyrina*, both described by MARSHALL, 1988) and four species are so far known to belong to this family (MARSHALL, 1988; WARÉN & BOUCHET, 1992). These species live on pieces of sunken driftwood or at hydrothermal vents, in fairly deep water, 1000–2000 m.

The species are characterized by:

- a rhipidoglossate radula
- a bipectinate ctenidium
- heavily ciliated areas on the tentacles
- an absence of epipodial tentacles
- the protoconch, if multispiral, is hyperstrophic.

The tentacular arrangement is still uncertain. Anatomical work on *Hyalogyrina* and the new genus described below is being carried out by G. Haszprunar.

Xenoskenea Warén & Gofas, gen. nov.

Type species: *Skenea pellucida* Monterosato, 1874, Mediterranean.

Diagnosis: Heterobranchs with *Vitrinella*-like, small, depressed, perfectly transparent, and almost smooth shell. Protoconch indistinctly hyperstrophic. Teleoconch with 2–3 evenly rounded whorls. Foot large, anteriorly expanded and shallowly bifurcate, posteriorly abruptly drawn out into a narrow, tentacle-like point. Snout large and cylindrical, with small tentacle distally on each side. Right corner of pallial cavity modified to a large pad, covering part of the preceding whorl. Gill bipectinate. Radula rhipidoglossate with formula $n \cdot 3 \cdot 1 \cdot 3 \cdot n$.

Description: See the description of *Xenoskenea pellucida*.

Etymology: *Xenos* (Greek), meaning “strange,” and *Skenea* (Skeneidae), an archaeogastropod genus with a shell similar to the type species.

Remarks: *Hyalogyra* differs from *Xenoskenea* in having a more depressed shell with more shallow suture. *Hyalogyra* also lacks the tentaclelike appendages on the snout and has three tentacles on the head.

Hyalogyrina also differs from *Xenoskenea* in lacking the distal appendages of the snout, by having short appendages between the cephalic tentacles or a long appendage laterally to the right cephalic tentacle, and by having a radula with a single row of lateral teeth on each side of the center.

The shell of *Xenoskenea* is very similar to that of *Cornirostra*, but has a flexous profile of the outer lip, instead of being straight and radial. Furthermore, *Cornirostra pellucida* has a long, slender right pallial tentacle, whereas *Xenoskenea* has a pad covering a part of the early part of the body-whorl, and *Cornirostra* has a bifurcate snout, whereas *Xenoskenea* has a cylindrical snout with two tentaclelike appendages. Also the radulae are widely different: *Xenoskenea* has a rhipidoglossate radula, whereas that of *Cornirostra* has the formula $1 \cdot 3 \cdot 1 \cdot 3 \cdot 1$.

There are some assumed archaeogastropods which are very similar to *Xenoskenea*, for example *Akritogyra* Warén, 1992 (provisionally in Skeneidae), but their larval shell has a proportionally larger initial part, which is not sunken in the center (see WARÉN, 1992:fig. 15A–F). This difference may, however, be due to lecithotrophic development in the species of *Akritogyra*. The external morphology of their soft parts and their anatomy is still largely unknown.

The radula and shell of a new species probably belonging to *Xenoskenea* were described from off Luanda (Angola) by RUBIO *et al.* (in press). The species was classified in *Hyalogyra* Marshall, but differs from *Xenoskenea pellucida* only in the shape of the central tooth. We therefore believe that this species belongs to *Xenoskenea*. The specimens were found on a dead fish from the bottom, and were assumed to be feeding on the carrion.

Xenoskenea pellucida was previously tentatively classified in *Skeneopsis* Iredale, 1915 (Skeneopsidae), a genus of littorinoidean affinity (PONDER, 1988). We illustrate the shell, protoconch, and radula of the type species for comparison (Figures 37–41).

Relying on shell morphology, PONDER (1990b:537) suggested that *Skenea pellucida* may belong to the Cornirotidae. This is not supported by the radular morphology.

The second European species of *Skeneopsis*, *S. sultanorum* Gofas, 1982, remains in *Skeneopsis*, based on observations of living animals (Gofas, unpublished data).

Xenoskenea pellucida (Monterosato, 1874)

(Figures 12, 13, 26–36)

Skenea pellucida ARADAS & BENOIT, 1874:159 (nom. nud.).

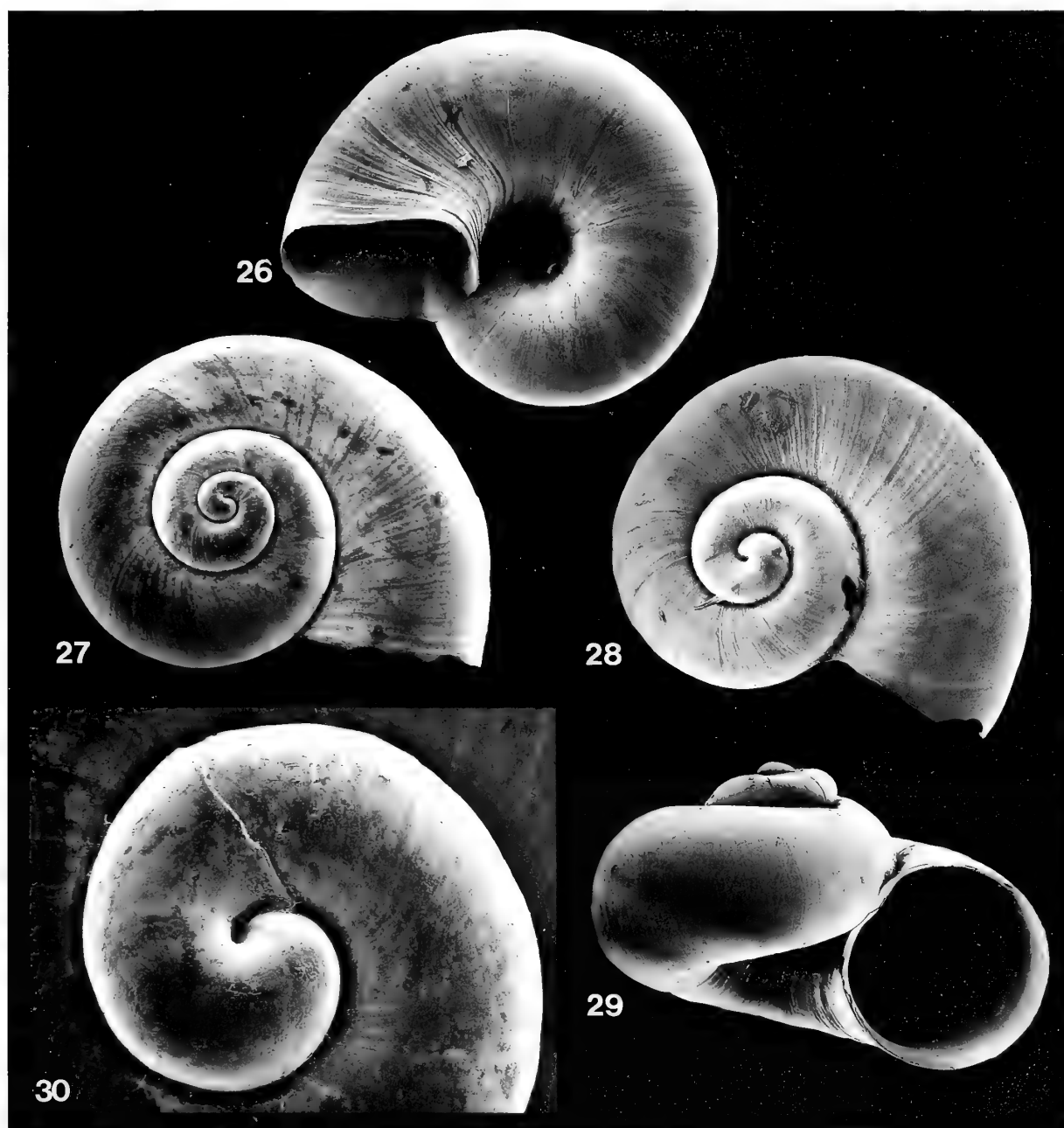
Skenea pellucida MONTEROSATO, 1874:263.

Skenea helicina Jeffreys MS, MONTEROSATO, 1874:263 (introduced in synonymy).

Skenea pellucidoides NORDSIECK, 1982:46.

Skeneopsis pellucida: GOFAS, 1982:232, fig. 8.

Skeneopsis? pellucida: PONDER, 1990b:537.



Explanation of Figures 26 to 30

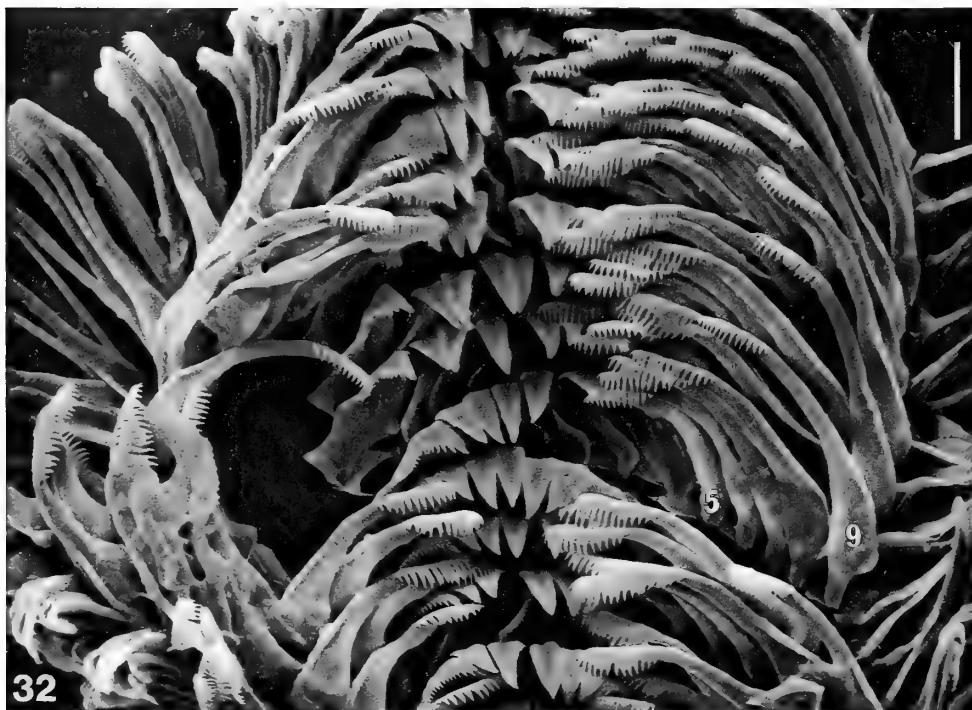
Figures 26–30. *Xenoskenea pellucida*, Tunisia, Bou Grara Sea. Figure 26. Basal view, diameter 1.56 mm. Figure 27. Apical view of adult specimen, diameter 1.59 mm. Figure 28. Apical view of young specimen, diameter 1.03 mm. Figure 29. Front view, adult specimen, diameter 1.64 mm. Figure 30. Larval shell, diameter 245 μ m.

Type materials: *Skenea pellucida*, lectotype (GOFAS, 1982) and 5 paralectotypes in MNHN. *Skenea pellucidoides*, holotype and 1 paratype, Balears, Ibiza, 50 m and 2 paratypes, Tunisia, Sfax, in Senckenbergisches Museum und Forschungsinstitut, Frankfurt a.M.

Type localities: *Skenea pellucida*, Sicily, Palermo; *S. pellucidoides*, Balears, Ibiza, 50 m.

Material examined: PORTUGAL, Algarve: Sagres harbor, 9–15 m, rocks with ooze, 4 shells (MNHN); Sagres, Ponta dos Caminhos, 23–33 m, 1 shell (MNHN); Sagres, Bay de Baleeira, 12–17 m, 1 shell (MNHN); Chenal d'Olhao, 3–7 m, in mud covered with *Zostera*, about 20 specimens (SMNH).

(Morocco) CEUTA: El Pineo, 35°52.6'N, 05°19.7'W, 9–10 m, 1 shell (MNHN).



Explanation of Figures 31 and 32

Figures 31, 32. Radula of *Xenoskenea pellucida*, Brucoli, Sicily. Figure 31. Detail of lateral and central teeth. Scale line 5 μ m. Figure 32. Overview, scale line 10 μ m.

MOROCCO: Near Oued er Rmel, 35°53.3'N, 05°30.2'W, 13 shells (MNHN).

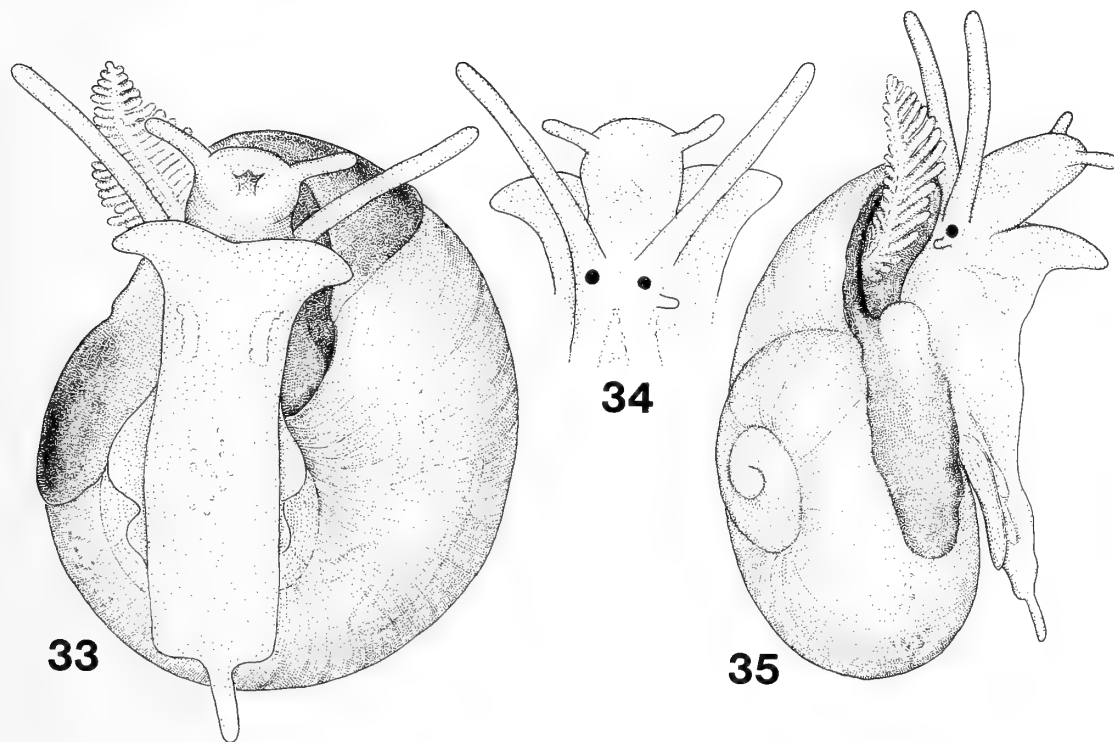
ALGERIA: Algiers, coll. Jeffreys, 1 shell (USNM 145049).

TUNISIA: Djerba, Borj Jillij, 0–8 m, among *Posidonia*, 2 shells (MNHN); Canal d'Ajim, 10–32 m, 5 shells (SMNH); Bou Grara Sea, littoral, 13 shells (MNHN).

ITALY: Gulf of Naples, coll. Jeffreys, 2 shells (USNM 185037); Sicily, no further details, 7 shells (SMNH); Sici-

ly, Trapani, from Monterosato, 4 shells (BMNH); Sicily, Magnisi, Palermo, coll. Jeffreys, 4 shells (USNM 185036); Sicily, S of Catania, Brucoli, *Posidonia* beds, 2 specimens (MNHN); Sicily, no further details, 6 + 10 shells, coll. Jeffreys (USNM 185035 and 202425).

FRANCE: Corsica, Baie de Calvi, algal washing, 10–40 m, 1 shell (SMNH).



Explanation of Figures 33 to 35

Figures 33–35. *Xenoskenea pellucida*, Portugal, Algarve, Ria de Olhão, Zostera bed, 3 m. Diameter of shell 1.7 mm.

GREECE: Pátrai lagunar area, 2 shells, *leg.* Nofroni (MNHN).

Distribution: Western and central Mediterranean, to southern Portugal, ca. 0–25 m, on muddy algal bottoms.

Redescription: The shell (Figures 26–29) is *Valvata*-like, small, fragile, completely transparent, smooth except for some growth lines. The larval shell (Figure 30) consists of about 0.75 whorl of rapidly increasing diameter, and its maximum diameter is 250 μ m. Its initial part is comparatively small and indistinctly hyperstrophic. The teleoconch consists of up to 2.3 whorls of almost circular cross section, sculptured by sharp, basally flexuous incremental lines. The suture is deep. The area in contact with the preceding whorl occupies 20–30° of the cross section of the whorl and makes a slight dent in the circular shape of the peristome. The umbilicus is deep and wide, and permits examination of the protoconch.

Dimensions: Maximum diameter 2.0 mm.

Radula (Figures 31, 32): The radula is rhipidoglossate with the formula $n \cdot 3 \cdot 1 \cdot 3 \cdot n$. The central tooth has diverging lateral supports and a slender, triangular cutting surface. The first lateral tooth is similar to the central but has a single lateral support and its inner side fits into a groove between the supporting ridge and “back” of the central tooth. The second lateral tooth is similar to the

first one. The third lateral tooth is much broader and the outer part of its cutting edge is serrated. The marginals are at least 10 in number, tall and slender, distally obliquely truncated, and deeply serrated.

Operculum (Figures 12, 13): Thin, colorless, and multispiral with central nucleus.

Soft parts (Figures 33–36): The foot is large and thin, anteriorly expanded and shallowly bifurcate. The sides are parallel, except the anterior and posterior extremities. Pos-

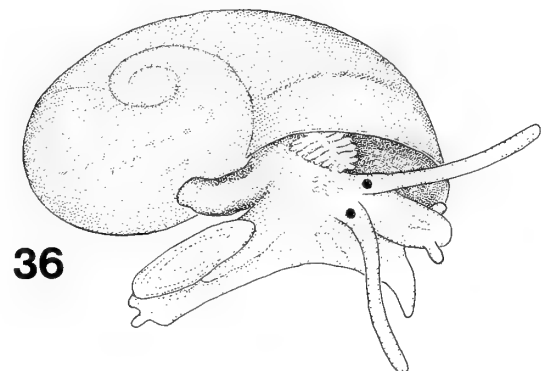
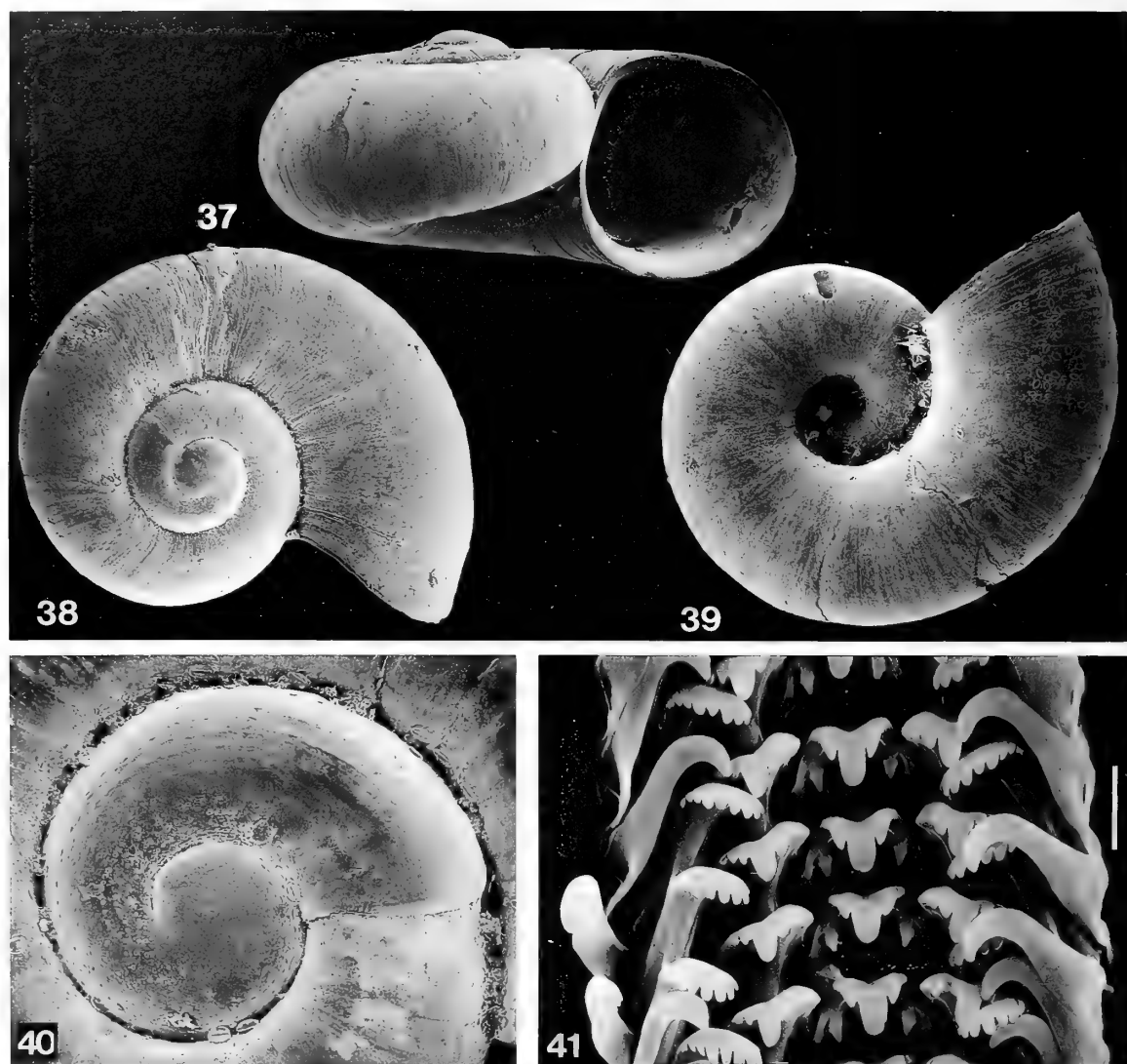


Figure 36

Xenoskenea pellucida, young specimen, Sicily, Brucoli, Posidonia bed, 3 m depth. Diameter of shell 1.1 mm.



Explanation of Figures 37 to 41

Figures 37–41. *Skeneopsis planorbis*. Figures 37–39. Shells. Ceuta, Anse Sarchal, intertidal. Diameters 1.3, 1.2, and 1.2 mm. Figure 40. Larval shell. Corsica, Calvi, Punta Revellata, intertidal. Diameter 290 μm . Figure 41. Radula. Norway, Finmark, intertidal. Scale line 10 μm .

teriorly it is abruptly drawn out into a narrow tentacle. The propodium is not externally differentiated. Just behind the corners of the foot, the propodium contains an opaque, yellowish mass of cells close to each side, and centrally there is a group of whitish, superficial spots consisting of glandular cells. The metapodium forms a bilobed skin fold between the operculum and the foot. The snout is large and cylindrical, apically truncated with a centrally situated mouth and a short, cylindrical tentacle on each side. The buccal mass and radula are visible through the transparent snout. The tentacles are long and slender, slightly tapering and lack sensory papillae. The black eyes are embedded in the center of the bases of the tentacles. The penis is small, situated just behind and slightly lateral to the right eye. The pallial margin is simple, dark gray

to black, and reflected over the edge of the peristome, especially at the left corner of the aperture. The right corner of the pallial cavity is modified to a large gray, black, or dark brown pad, covering a part of the preceding whorl. The edge of the mantle and the apertural pads are superficially dark gray; the upper part of the snout and the tentacles are only slightly tinged with the same color. The gill is bipectinate with more than 20 pairs of leaflets. It is attached basally, and protrudes from the pallial cavity when the animal is crawling. In live specimens the food-string could be observed in the upper part of the intestine, rotating clockwise.

Remarks: *Xenoskenea pellucida* appears to be a rare species, judging from the literature, but this is probably a

collecting bias because it lives on shallow, muddy seagrass-and algal bottoms, which are only rarely examined for this small size range of gastropods.

The shell of *Xenoskenea pellucida* is just as featureless as the soft parts are characteristic, but there are no species known in shallow Mediterranean waters with which it is likely to be confused.

CARROZZA (1976:fig. 7) used the name *Skenea pellucida* for an unusually smooth specimen of *Skeneopsis planorbis* (Fabricius, 1780).

Xylodiscula boucheti Warén, 1992 (Xylodisculidae, Heterobranchia) is superficially similar but has a flatter spire and broader umbilicus, and lives in deeper water. It has a very different radula with no central tooth.

ACKNOWLEDGMENTS

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Three new *Halgerda* species (Doridoidea: Nudibranchia: Opisthobranchia) from Guam

by

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Abstract. *Halgerda tessellata* (Bergh, 1880) is reported from Guam and Pohnpei within the Micronesian area and three new species of *Halgerda* are described. Two are compared with *H. aurantiomaculata* (Allan, 1932) and *H. terramtuentis* Bertsch & Johnson, 1982, both previously described white tuberculate forms. The third is compared with the type species of the genus, *H. formosa* Bergh, 1880.

INTRODUCTION

The genus *Halgerda* Bergh, 1880a (= *Dictyodoris* Bergh, 1880b) contains dorids with a somewhat smooth, stiff gelatinous texture with a reticulate pattern of dorsal ridges which may or may not have tubercles at their points of juncture. Recent discussion of the genus can be found in RUDMAN (1978) and WILLAN & BRODIE (1989). Since 1969, 10 species of *Halgerda* have been collected on Guam, including one dredged from 120 m. Six of the species are represented by only one or two specimens in the authors' collection. Of the remaining four, one has been previously described, BERGH (1880b), and three are described in this paper.

SPECIES DESCRIPTIONS

Halgerda tessellata (Bergh, 1880)

(Figures 1-3)

Dictyodoris tessellata BERGH, 1880b:75-78, pl. C, figs. 11-12; pl. F, figs. 22-23; ELIOT, 1905:229-230; BURN, 1975:515.

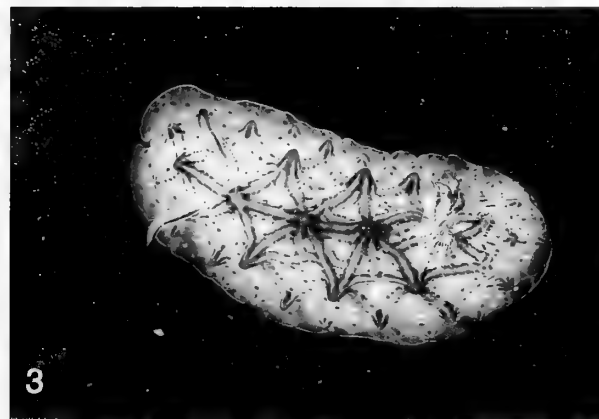
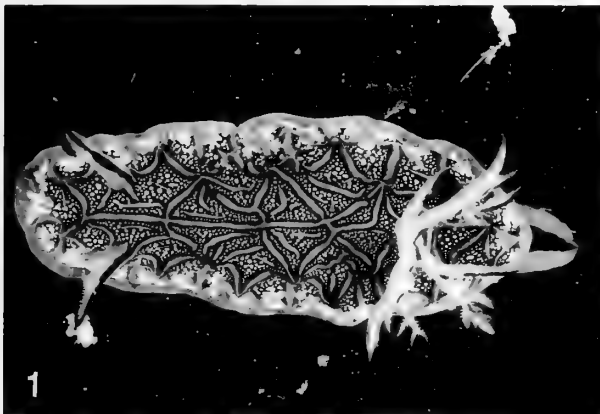
Halgerda tessellata (Bergh): RUDMAN, 1978:65-67, figs. 4C-D, 6; WILLAN & COLEMAN, 1984:38-39, 52.

Distribution: *Halgerda tessellata* was originally described from Palau (7-8°N, 134°E) in the Western Caroline Islands. *Halgerda tessellata* has also been reported from Australia (BURN, 1975), Madagascar (ELIOT, 1905), and Kenya (RUDMAN, 1978). Since 1969, 87 specimens of *H.*

tessellata have been found on Guam (13°N, 145°E) and an additional two on Pohnpei (7°N, 158°E) in the Federated States of Micronesia. The average depth has been 8 m, with the deepest found at 15 m. Two have been found on the reef flat. The largest measured specimen was 33 mm. The records from Guam and Pohnpei extend the range both north and east in the Micronesian area. The only other *Halgerda* recorded with such a wide Indo-Pacific distribution is *H. wasinensis* Eliot, 1904. It has been reported from the Tanzanian-Kenyan area of east Africa (ELIOT, 1904; RUDMAN, 1978) and the Marshall Islands (JOHNSON & BOUCHER, 1983).

Color: In most specimens, the body color, as seen from the foot, underside of mantle and mantle margin, varies from yellow to yellow-orange (Figures 1, 2). Except for a broad marginal band, most of the dorsum is covered by dark brown pigment. The brown pigment is less dense over the ridges giving them a mustard yellow to orange-brown appearance. Scattered opaque white dots occur in the depressions between the ridges. These dots become denser toward the outer edge of the brown. Scattered dark brown spots are on the sides of the foot and underside of the mantle. There is also a broad dark brown line on the mid-dorsal part of the tail. The rhinophores are translucent white with a dark brown posterior streak. The lamellae are dark brown. The branchia are white with some of the upper surface of the rachis dark brown. The ridge coloring is not as red as that shown on the color plate in WILLAN & COLEMAN (1984:39, fig. 118). One of the specimens from Pohnpei (Figure 3) had a translucent white rather than yellow body and less of the brown pigment.

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Explanation of Figures 1 to 3

Figures 1–3. *Halgerda tessellata*. Figure 1. 14-mm specimen, Guam, Bile Bay, 14 m depth, 13 June 1971. Figure 2. 23-mm specimen, Guam, Bile Bay, 2 July 1984. Figure 3. 33-mm specimen, Pohnpei, 8 m depth, 17 October 1987.

Halgerda guahan Carlson & Hoff, sp. nov.

(Figures 4–9)

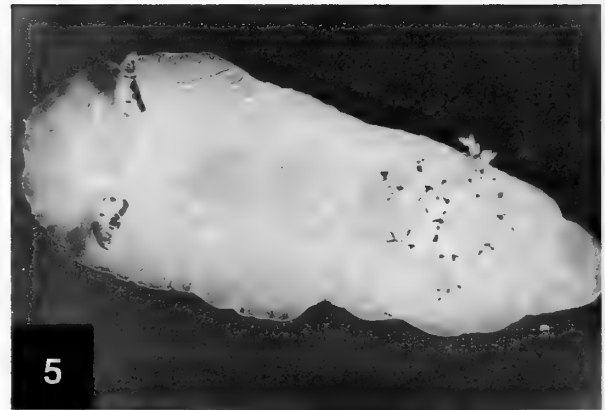
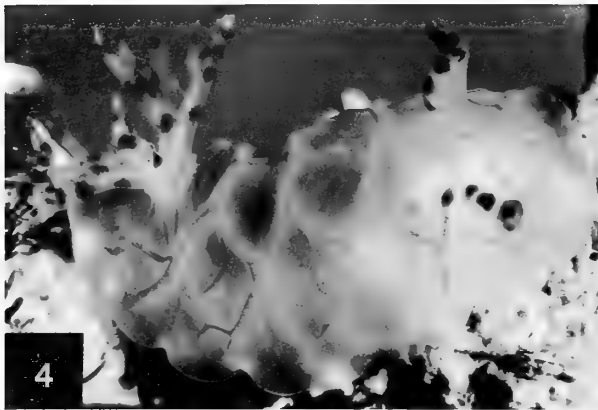
Halgerda graphica Basedow & Hedley: CARLSON & HOFF, 1973:6, fig. 5 (misidentification).

Specimens: Since 1969, 59 specimens of *Halgerda guahan* have been found on Guam. The average depth was 8 m, the maximum 15 m. One specimen was found on the reef flat. The average length of those measured was 43 mm, the longest 64 mm.

Type material: Holotype (64 mm), Bishop Museum, Honolulu, BPBM 209916, reef flat, Cetti Bay, Guam, 18 June 1988, Carlson and Hoff. Paratype (47 mm), Bishop Museum, Honolulu, BPBM 209917, 11 m depth, Bile Bay, Guam, 16 March 1991, Carlson and Hoff. Material dissected: 1 specimen, 32 mm, 15 m depth, Agat, Guam, Carlson and Hoff, 21 March 1969; 1 specimen 35 mm, Bile Bay, Guam, Carlson and Hoff, 17 December 1978; 1 specimen 53 mm, 12 m depth, Bile Bay, Guam, Carlson and Hoff, 29 October 1982; 1 specimen, 45 mm, 9 m depth, Bile Bay, Guam, Carlson and Hoff, 16 March 1991. Rad-

ulae of the 35-mm and 45-mm specimens were used for scanning electron microscopy.

External morphology: The living animals (Figures 4, 5) are ovate. A 38-mm specimen had a maximum width of 21 mm, others were 46 × 25 mm and 53 × 26 mm. The body has a firm gelatinous texture, as is found in all other members of the genus. It is convex, sloping gradually from the thin mantle margin to the mid-dorsum. The broad, flaring mantle is slightly irregular and usually lies along the substrate when the animal is crawling. The dorsum has a series of low ridges and depressions with no tubercles. A central ridge extends from just in front of the rhinophores almost to the branchia. Two polygonal ridged areas are on either side of this medial ridge and an incomplete polygonal area contains the rhinophores. Other ridges extend transversely from the polygons toward the mantle margin. Shallow depressions occur within each polygon and between the transverse ridges. The ridges have 16 major points of convergence; four along the midline and six on either side. The foot (Figure 6) is a little over one-third of the width of the animal (8 mm for a 21 mm wide



Explanation of Figures 4 and 5

Figures 4, 5. *Halgerda guahan* sp. nov. Figure 4. 32-mm specimen, Guam, Agat Boat Channel, 15 m depth, 21 March 1969. Figure 5. 48-mm specimen, Guam, Anae Island, March 1991.

specimen) and it ends in a rounded tail that is sometimes visible when the animal is crawling. The anterior of the foot has a transverse groove with the upper lamina split in the middle. The oral tentacles are digitiform.

The base of the rhinophores is short and stocky; the club is thin and angled posteriorly. The branchia has four gills; the posterior two being divided about one-third of the way up from the base. The branchial and rhinophoral sheaths are low and simple.

The body is translucent white, almost transparent on the mantle margin. The pinkish brown to purplish brown color of the viscera is visible through the dorsal surface.



Figure 6

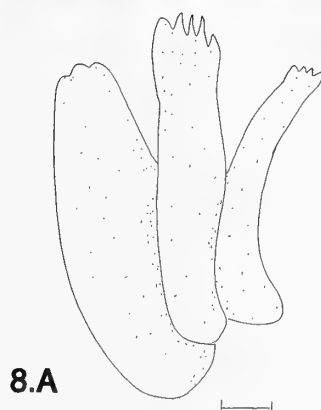
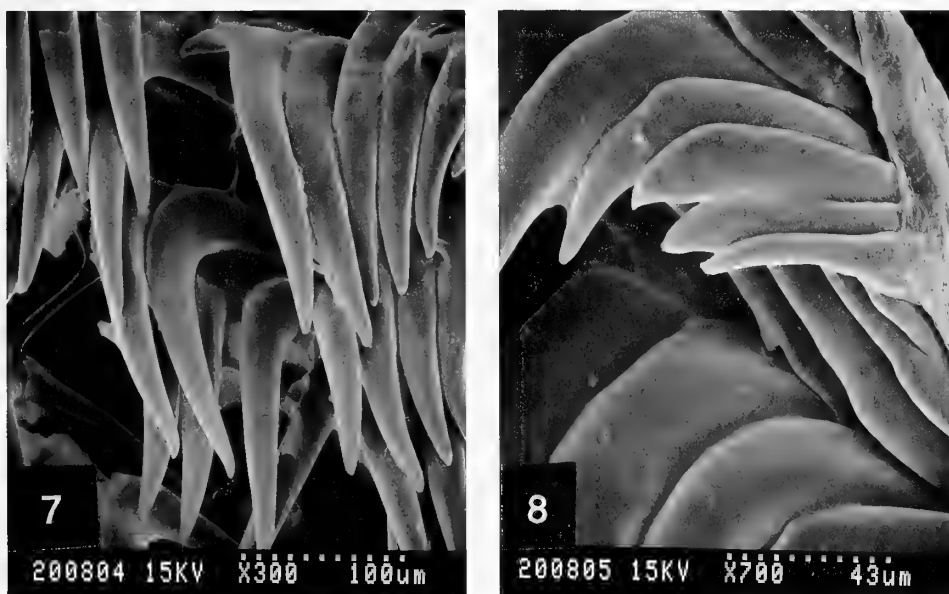
Halgerda guahan sp. nov., ventral view, 48-mm living specimen.

The mantle margin is edged by a thin, opaque white line. All ridges are edged in yellow. Single, irregular, curved yellow lines appear within the depressions. No lines extend to the edge of the mantle. The rhinophores are translucent white with brown spots on the base and lamellae. On some specimens the posterior of the rhinophoral base has a broad brown line, which continues as brown streaks on the posterior parts of the lamella. The rhinophoral sheath is edged in yellow. The branchia are translucent with scattered white extending up the rachis and on the tips. Sparse brown spots also appear on the branchia. The branchial sheath is white with yellow lines that extend up from the body. The underside of the body, foot, and oral tentacles are translucent white. Some specimens have a small brown dot between the upper and lower lamina at the anterior of the foot.

Specimens possessing color variations have been found. These variations appear to be the result of damage to the dorsal surface, which causes the yellow lines on the ridges to become broken and irregular.

Specimens preserved in alcohol have retained the brown pigment but not the yellow. In one specimen, which had been fixed in 5% formalin and stored in alcohol for two years, the ridges became pink. It can also be seen on the preserved specimens that the yellow lines within the dorsal depressions actually covered low ridges.

Internal morphology: The sac of tissue enclosing the viscera, which appears dark in slides of living specimens, is transparent with brown flecks. With the sac opened dorsally, the large oval stomach, the intestine, the digestive gland mass, and the prostate-covered bursa copulatrix are visible. With the blood gland and nerve ring removed, the white oral tube can be seen curving to join the heavy muscular buccal bulb. With the stomach moved slightly to the right, the broad curved radular sac can be seen extending from the ventral posterior of the buccal bulb. The esophagus exits from the buccal bulb, makes a dorsal



8.A

Explanation of Figures 7 and 8

Figures 7, 8. *Halgerda guahan* sp. nov. Figure 7. Scanning electron micrograph of middle lateral teeth, 45-mm specimen. Figure 8. Scanning electron micrograph of outermost lateral teeth, 45-mm specimen. Figure 8A. Camera lucida drawing of outermost lateral teeth, 32-mm specimen. Scale = 10 μ m.

loop and enters the stomach ventrally. The intestine exits from the anterior of the stomach and curves around the right side of the digestive gland and continues posteriorly to the anus. From the dorsal view, the top of the brownish prostate-enclosed bursa copulatrix and the albumen/mucous (female) gland complex can be seen to the right and anterior to the stomach. The aorta passes from the blood gland, crosses and is attached to the top of the prostate-covered bursa copulatrix. It continues under the intestine and extends posteriorly to the heart at the anterior base of the branchia.

The radular formulae for 32-mm and 45-mm adult specimens were $50 \times 49.0-49$ and $46 \times 45-47.0-45-47$ respectively. All teeth except the outer three laterals are simply hamate with a flange on the inner edge. In the 32-

mm specimen, the inner 20 teeth were small and gradually increased in size toward the center of the half row (Figure 7). There were 26 large teeth of approximately the same size and then three small outer laterals. The innermost lateral was smaller than the outermost. The scanning electron micrograph shows the outermost laterals to be flattened plates with the outer two having slightly irregular apices (Figure 8). When viewed with a compound microscope the innermost of these three teeth appeared irregular at the apex, the penultimate tooth appeared slightly denticulate, and the outermost was very thin and apically denticulate (Figure 8A).

Within the reproductive system (Figure 9), the hermaphroditic duct connects to the ampulla posterior to the genital mass. The broad ampulla appears as a convoluted,

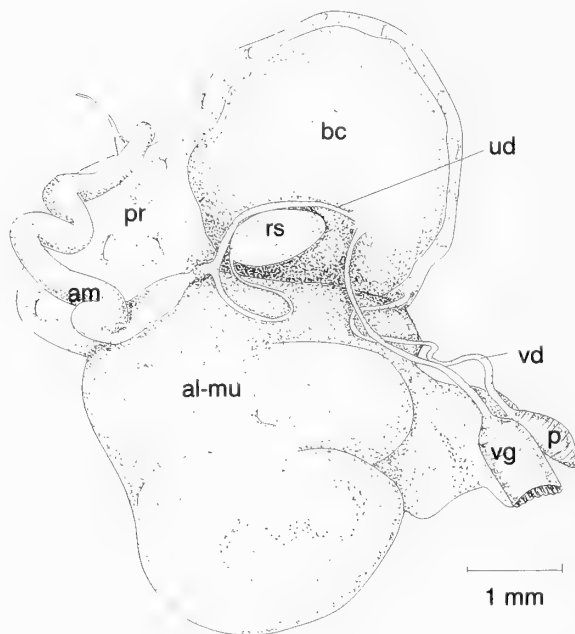


Figure 9

Halgerda guahan sp. nov., Reproductive system: al-mu, albumen-mucous gland; am, ampulla; bc, bursa copulatrix; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; vd, vas deferens; vg, vaginal duct.

somewhat flattened tube at the posterior of the prostate and the albumen/mucous gland complex. It narrows and enters the genital mass at the gland complex, where it joins the prostate gland. The whitish prostate gland ensheathes and folds down under the bursa copulatrix. The actual point of entry of the duct from the ampulla was not observed. A narrow duct arises from the same area, and divides into two ducts; one, the uterine duct, extends for-

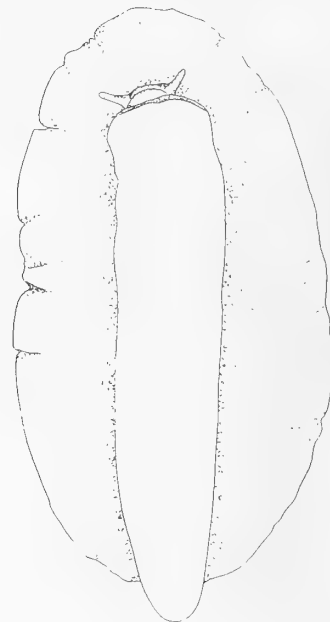
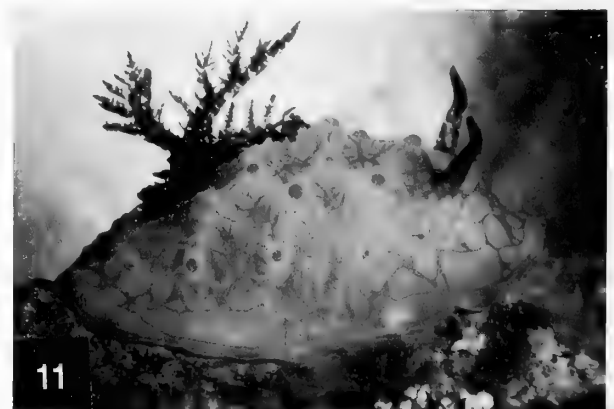
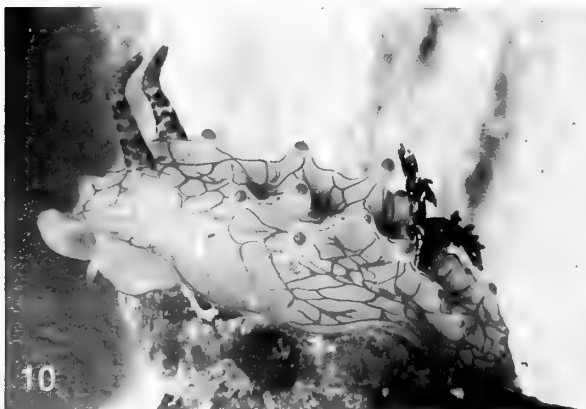


Figure 12

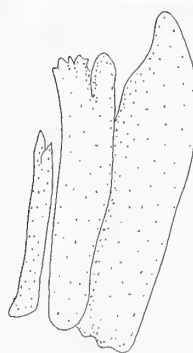
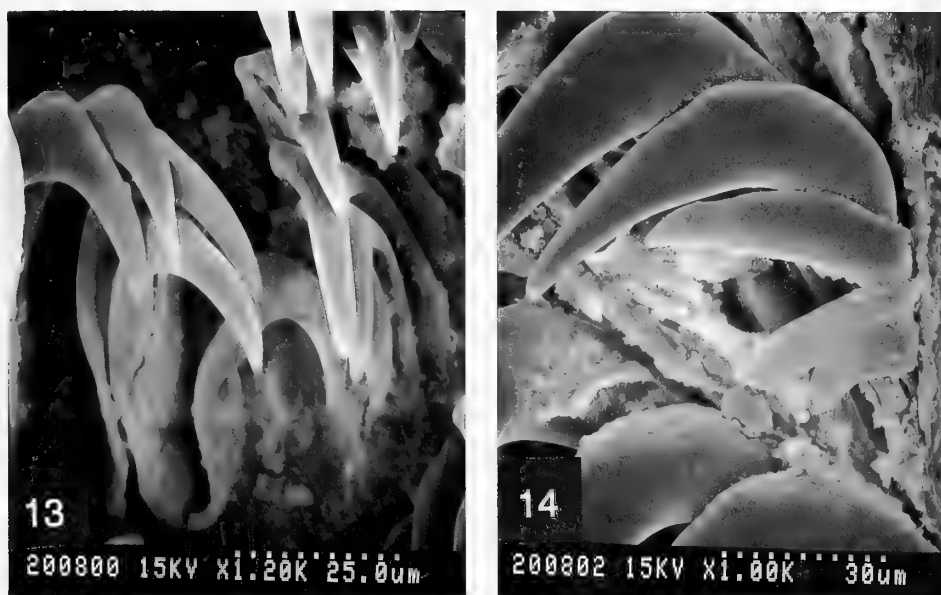
Halgerda malesso sp. nov., ventral view, 65-mm living specimen.

ward, where it enters the bursa copulatrix; the other leads to the receptaculum seminis, which is embedded in the prostate gland between the bursa copulatrix and the female gland complex. The long thin tube to the ovoid receptaculum seminis forms a loop along the gland complex and joins the receptaculum seminis posteriorly. Adjacent to the entry of the uterine duct into the bursa copulatrix is the vaginal duct, leading to the vagina which is enclosed in a muscular sheath with the smaller penis. The vagina has a series of longitudinal folds. The long sinuous vas deferens



Explanation of Figures 10 and 11

Figures 10, 11. *Halgerda malesso* sp. nov. Figure 10. 64-mm specimen, Guam, Anae Island, 8 m depth, 27 April 1969. Figure 11. 48-mm specimen, Guam, Toguon Bay, 18 m depth, 11 April 1969.



14.A

Explanation of Figures 13 and 14

Figures 13, 14. *Halgerda malesso* sp. nov. Figure 13. Scanning electron micrograph of innermost lateral teeth, 55-mm specimen. Figure 14. Scanning electron micrograph of outermost lateral teeth, 55-mm specimen. Figure 14A. Camera lucida drawing of outermost lateral teeth, 64-mm specimen. Scale = 10 μ m.

extends from the small penis to the prostate where it ensheaths the bursa copulatrix. A broad extension from the female gland mass leads to the genital opening, where it terminates in the oviduct. The vagina, penis, and oviduct share a common opening through the body wall.

Discussion: *Halgerda guahan* differs from previously described white and orange species of *Halgerda* in that it lacks tubercles, has an uncolored mantle and foot margin, and has a comparatively simple pattern of lines on the dorsum. Internally, the narrow vagina and penial sac enclosed in a muscular sheath differ from the large vagina and large penial sac of both *H. aurantiomaculata* (Allan, 1932) and *H. terramtuensis* Bertsch & Johnson, 1982.

The specific name *guahan* is the Chamorro (*i.e.*, the indigenous people of Guam) name for the island of Guam.

Halgerda malesso Carlson & Hoff, sp. nov.

(Figures 10–15)

Specimens: Since 1969, 117 specimens of *Halgerda malesso* have been found on Guam and an additional six on the island of Sarigan (17°N, 146°E) in the Northern Mariana Islands. The average depth was 9 m, with the deepest recorded, 18 m. The average length of those measured was 48 mm, the longest was 65 mm.

Type material: Holotype (49 mm), Bishop Museum, Honolulu, BPBM 209914, 14 m depth, Bile Bay, Guam, 24 April 1991, Carlson and Hoff. Paratype (65 mm), Bishop Museum, Honolulu, BPBM 209915, 15 m depth, Bile Bay, Guam, 20 April 1991, Carlson and Hoff.

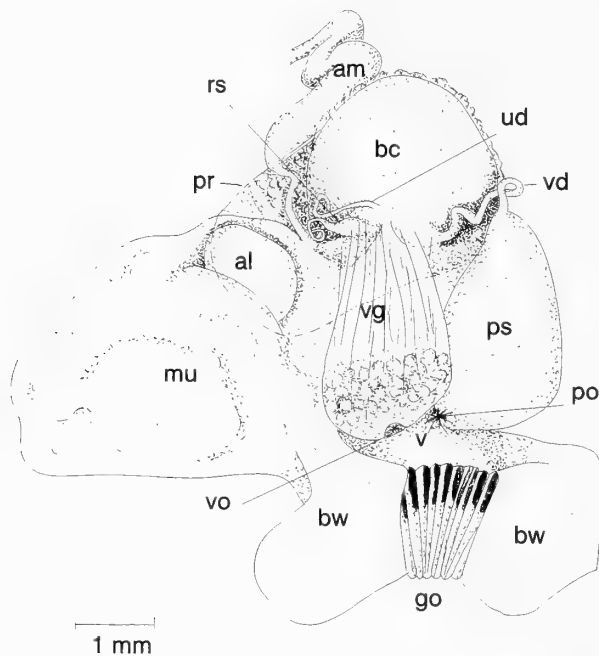


Figure 15

Halgerda malesso sp. nov. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; bw, body wall; go, genital opening; mu, mucous gland; po, penial opening; pr, prostate; ps, penial sheath; rs, receptaculum seminis; ud, uterine duct; v, vestibule; vd, vas deferens; vg, vagina; vo, vaginal opening.

Material dissected: 1 specimen, 64 mm, 8 m depth, Ana'e Island, Guam, Carlson and Hoff, 27 April 1969; 1 specimen 55 mm, 7 m depth, Bile Bay, Guam, Carlson and Hoff, 13 July 1988; 1 specimen, 60 mm, 14 m depth, Bile Bay, Guam, 24 April 1991. Radulae of the 60-mm and 55-mm specimens were used for scanning electron microscopy.

External morphology: The living animals (Figures 10, 11) are ovate with a broad, thin, slightly undulating mantle edge. A 55-mm specimen was approximately 30 mm wide at the broadest point. As is true of other species of *Halgerda*, the body texture is gelatinous, smooth, and firm. The dorsum has three distinct, irregular, longitudinal ridges with elevated tubercles and numerous depressions. The median ridge, with the highest tubercles, extends from in front of the rhinophores almost to the branchia. There are four major tubercles on this ridge, one anterior to the rhinophores and three between the rhinophores and branchia. The lateral ridges extend from behind the rhinophores to either side of the branchia. A few tubercles are scattered outside the lateral ridges. The foot (Figure 12) is about one-third of the body width. The anterior end is grooved with the upper lamina split. The rounded tail is sometimes visible when an animal is crawling. Oral tentacles appear short and rounded when an animal is at rest; digitiform when crawling.

The rhinophores are long and tapering, with the club

angling posteriorly. The club and base are about equal in length. The branchia has four gills with numerous large pinnae. In one specimen the posterior two gills were split about two-thirds of the way up from the base. The branchial and rhinophore sheaths are low and smooth. The anus is long and thin.

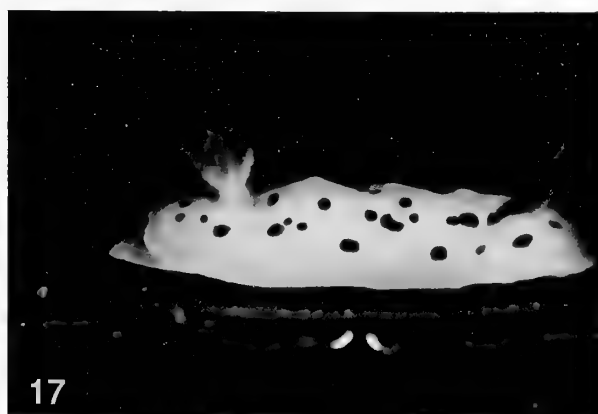
The body is translucent white with numerous irregular networks of orange lines extending over most of the dorsal surface. These networks are most predominant in the depressions adjacent to the mid-dorsal ridge, where they may fuse, creating pale patches of orange. They may or may not join between depressions. The mantle margin is translucent white with two fine submarginal orange lines. Often these lines attach to the lines on the higher part of the dorsum. The apex of the tubercles is orange. The orange lines on the body do not extend to the tips of the tubercles, thus leaving an unpigmented area surrounding the orange tips. The rhinophores are translucent white with brown spots, brown lamella, and white tips. The branchia is translucent white with brown spots and white tipped brown pinnules. The anus is light brown with darker brown spots and a white tip. The foot is white, rimmed in orange. The oral tentacles have an orange tip. The orange lines toward the edge of the dorsum can be seen from below.

Specimens preserved in alcohol are whitish and have retained the brown pigment on the rhinophores and branchia. A recently preserved specimen retained some yellow on the largest tubercles. In some areas, fine white lines occur where there were orange lines in the living specimen. This is especially noticeable of the submarginal orange lines.

Internal morphology: The internal anatomy appears to be the same as that of *Halgerda guahan*, as well as having the transparent visceral sac with sparse brown flecks.

The radular formulae for 64-mm and 55-mm adult specimens were $67 \times 61.0 \cdot 61$ and $51 \times 71.0 \cdot 71$ respectively. All teeth except the outer three laterals are simply hamate, with a flange on the inner edge. The half row has very small inner teeth (Figure 13) gradually increasing in size toward the center and decreasing toward the outer laterals. The innermost tooth is larger than the outermost lateral. A scanning electron micrograph (Figure 14) of the 55-mm specimen revealed that the three outer laterals are flattened plates with irregularities at the apex of the outer two. When viewed with a compound microscope (64-mm specimen), the innermost of these was smooth; the penultimate was denticulate with one large thumblike denticle on the inner edge and four to five denticles along the apex; the outermost appeared bifid (Figure 14A).

The general arrangement of the genital system (Figure 15) is the same as that described for *Halgerda guahan*, but it differs in detail. The hermaphroditic duct connects to the ampulla posterior to the genital mass. The broad ampulla appears as a convoluted, somewhat flattened tube at the posterior of the prostate and the albumen/mucous gland complex. It narrows and enters the genital mass at



Explanation of Figures 16 and 17

Figures 16, 17. *Halgerda brunneomaculata* sp. nov. Figure 16. 23-mm specimen, Guam, Sella Bay, 4 November 1972. Figure 17. 16-mm specimen, Guam, Cocos Reef, 3 m depth, 13 September 1970.

the gland complex, where it joins the prostate gland. The whitish prostate gland ensheathes, and folds down under, the bursa copulatrix. Two ducts arise adjacent to the area where the ampullar duct enters the genital mass. One, the uterine duct, makes a loop and extends forward, where it enters the bursa copulatrix and the prostate gland. The other long, thin duct forms a loop and extends to the receptaculum seminis, which it joins posteriorly. The receptaculum seminis is embedded in the prostate gland between the bursa copulatrix and the female gland complex and is partially covered by the vaginal duct. The receptaculum seminis is small and ovoid with a narrow distal section. Adjacent to the uterine duct entry into the bursa copulatrix is the vaginal mass. The vagina has a large glandular layer near its opening. The sinuous vas deferens joins the prostate where it covers the bursa copulatrix and extends to the large penial sac, which opens into a common vestibule with the vagina. The penis and vagina are not muscularly connected. A broad extension from the female gland mass leads to the genital opening, where it terminates in the oviduct. The common opening through the body wall for the vagina, penis, and oviduct is lined with dark spotted, longitudinal folds.

Discussion: *Halgerda malesso* can be compared with *H. aurantiomaculata* (Allan, 1932) and *H. terramtuentis* Bertsch & Johnson, 1982, both white, orange-marked, tuberculate species. Externally, *H. malesso* lacks the colored mantle margin as well as the color on the ridges between tubercles of these two species. It also differs from *H. terramtuentis* in that the tubercles are capped in orange rather than white. All three species have a large penial sac and glandular structures on the vaginal duct, although the relative shape of the duct varies. WILLAN & BRODIE (1989) described folds in the vagina of *H. aurantiomaculata*, whereas in *H. malesso* folds are found only in the body wall.

The specific name *malesso* is the Chamorro name of the village in southern Guam where most of the specimens have been found.

Halgerda brunneomaculata
Carlson & Hoff, sp. nov.

(Figures 16–21)

Specimens: Since 1969, 40 specimens of *Halgerda brunneomaculata* have been found on Guam and two on Sarigan in the Northern Mariana Islands. All but one specimen were found at a depth of 3 m or greater, the deepest being 21 m. The average length of those measured was 13 mm, the longest was 23 mm.

Type material: Holotype (13 mm), Bishop Museum, Honolulu, BPBM 209918, 4 m depth, Bile Bay, Guam, 29

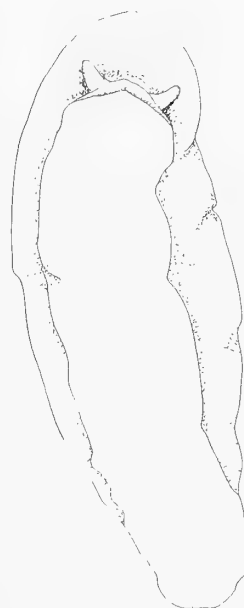
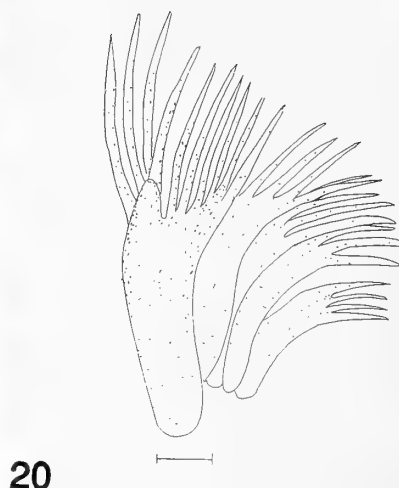


Figure 18

Halgerda brunneomaculata sp. nov., ventral view, 13-mm specimen.



Explanation of Figures 19 and 20

Figures 19, 20. *Halgerda brunneomaculata* sp. nov. Figure 19. Scanning electron micrograph of innermost lateral teeth, 23-mm specimen. Figure 20. Camera lucida drawing of outermost lateral teeth, 13-mm specimen. Scale = 10 μ m.

September 1990, Carlson and Hoff. Paratypes (11, 12 mm) Bishop Museum, Honolulu, BPBM 209919, 9 m depth, Toguon Bay, Guam, 16 April 1972, Carlson and Hoff.

Material dissected: 1 specimen, 23 mm, Sella Bay, Guam, Carlson and Hoff, 4 November 1972; 1 specimen, 13 mm, 2 m depth, Bile Bay, Guam, Carlson and Hoff, 11 January 1987; 1 specimen 13 mm, 18 m depth, Bile Bay, Guam, Carlson and Hoff, 27 June 1991. Radulae of 23-mm and 13-mm specimens were used for scanning electron microscopy.

External morphology (Figures 16, 17): *H. brunneomaculata* is elongate-ovate. A 16-mm specimen was about 4 mm in width. The dorsum is marked by a pattern of low ridges. The ridges form a series of irregular polygons on either side of the midline, sometimes partially crossing it. The ridges are slightly higher at their points of juncture, but tubercles are not present. The foot (Figure 18) is relatively broad and about two-thirds the width of the animal. As with the preceding two species, the anterior of the foot has a transverse groove. The broad, rounded tail extends beyond the posterior mantle edge. The oral tentacles are digitiform.

The rhinophores are lamellate for approximately half of their length, with the broadest lamellate part being about the same width as the heaviest part of the base. There is a slight conical tip that is most noticeable in smaller specimens. Only one specimen showed posterior angulation of the club. The branchia is made up of four pinnate branches. On one specimen, the tip of the two anterior branches

was divided. Both rhinophores and branchia have a smooth low sheath.

The ground color of *Halgerda brunneomaculata* is a pale translucent yellow. The ridges are marked with a darker opaque yellow, which becomes less intense toward the mantle edge and terminates in a series of dots rather than a solid line. On one 13-mm specimen, the body color was dark yellow, presenting no contrast between the ridge and body color. Most of the depressions formed by the ridges have a single, dark brown spot, although a few specimens have scattered spots. Irregular brown spots occur on the top of the tail and sides of the foot. A line of brown spots occurs at the juncture of the mantle and foot. The viscera, as viewed through the dorsal surface, appears dark in some specimens and light in others. The rhinophores are translucent white with dark brown lateral stripes. The branchia is translucent white with a dark brown stripe on the upper side of the rachis. The rhinophore and branchial sheaths are unmarked.

Specimens preserved in alcohol vary from pale yellow to tan. None of the yellow on the ridges is retained. The brown spots and brown lines on the rhinophores and branchia are retained in some specimens and almost completely lost in others. Some of the brown pigment that is retained comes off easily when the specimen is handled, a characteristic also noted by BASEDOW & HEDLEY (1905:152) in *Halgerda graphica*.

Internal morphology: The general arrangement is similar to that described above for *Halgerda guahan* and *H. ma-*

lesso, with one major exception. In the preceding two species, the main component of the genital system that is visible when the animals are opened dorsally is the prostate-covered bursa copulatrix. The genital system of *H. brunneomaculata* is twisted about 90 degrees to the left, which hides the bursa copulatrix under part of the female gland mass and digestive and buccal organs, leaving part of the female gland mass visible.

For two 13-mm and one 23-mm adult specimens, the radular formulae were $37 \times 30-32 \cdot 0 \cdot 30-32$, $48 \times 35 \cdot 0 \cdot 35$, and $51 \times 29 \cdot 0 \cdot 29$ respectively. All except the outer five teeth are simply hamate with a flange on the inner edge. In the 13-mm specimen, the inner five teeth (Figure 19) were comparatively small and gradually increased in size. Teeth six through 12 increased rapidly, and then the remaining laterals increased gradually to the largest teeth near the outer end of the half row. The innermost lateral was smaller than the outermost lateral. The outer five teeth (Figure 20) were small, flattened, and apically pectinate. The innermost of these small teeth had a large pectinate denticle on its inner edge. Scanning electron micrographs of the outermost lateral teeth were not successful because the pectinations folded over during dehydration.

As noted above, the genital mass of *Halgerda brunneomaculata*, *in situ*, appears quite different from that of *H. guahan* and *H. malesso* because of the orientation to the left. Otherwise the relationship of the parts of the system is much the same (Figure 21). The small hermaphroditic duct connects to the ampulla ventrally at the posterior of the genital mass. The broad, somewhat flattened, ampulla has a large fold, then narrows before entering the albumen/mucous gland complex. The small uterine duct arises anterior to the entry of the ampullar duct and extends to, and connects with, the bursa copulatrix. The large prostate narrows where it folds over to partially enclose the small bursa copulatrix. The subovoid receptaculum seminis, which is almost as large as the bursa copulatrix, is partially embedded in the prostate on one side and lies against the bursa copulatrix on the other. It is joined to the uterine duct by a short, thin tube. The uterine duct gives the appearance of winding over the surface of the bursa copulatrix and it exits as the vaginal duct, near the area where the narrow part of the prostate folds over the bursa copulatrix. This vaginal duct is quite sinuous and broadens to form the vagina. The sinuous vas deferens exits from the narrowest part of the prostatic fold and leads to the elongate penial sheath, which joins the vagina before reaching the opening through the body wall. A large extension from the female gland mass, the oviduct, is adjacent to the penis and vagina, where the common opening is situated. This opening is lined with longitudinal folds.

Discussion: Only one other species of *Halgerda* has been described that has a pale yellow ground color, *H. formosa* Bergh, 1880, the type species of the genus. The original color notes from Dr. Koerbl state, "gelblichweiss mit or-

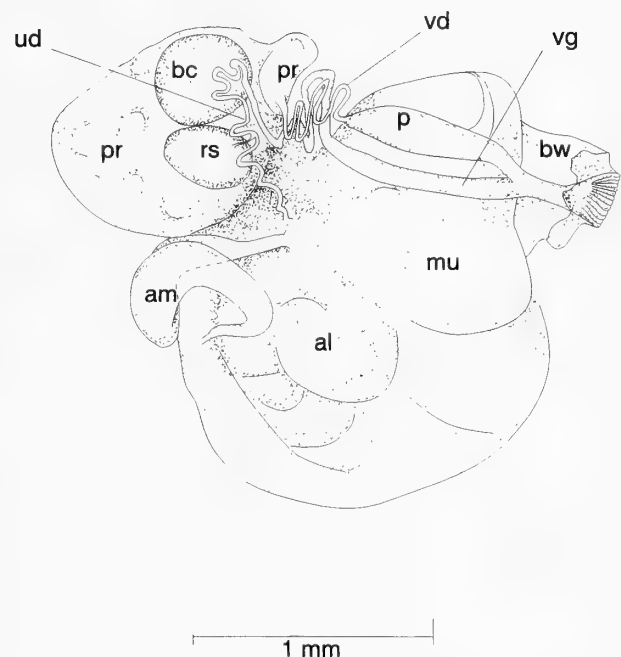


Figure 21

Halgerda brunneomaculata sp. nov. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; bw, body wall; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; vd, vas deferens; vg, vagina.

angelegten Streifen und schwarzen Punkten am Rücken, sowie mit schwarzen Rhinophorien" (BERGH, 1880a:191). When Bergh worked on the preserved animal he found only one black spot and also reported a black band on the midline of the tail. We assume that much of the dark pigmentation had been lost in the preserved animal Bergh examined, as is common with many of our specimens. Externally, *H. formosa* and *H. brunneomaculata* appear to be similar in terms of body color, darker ridge coloration, and the presence of dark spots. The main differences are the presence of the dark band on the tail of *H. formosa* and the lack of dark pigmentation on the rhinophoral base. The latter could be from loss of pigmentation in preservative. Internally, Bergh describes a chocolate-brown visceral sac, whereas that for *H. brunneomaculata* is translucent with sparse brown flecks. The oral tube, spotted in *H. formosa*, is unmarked in *H. brunneomaculata*. The number of pectinate laterals is different in the two species: two for *H. formosa* and five for *H. brunneomaculata*. The denticles on the laterals are also much shorter in *H. formosa* than in *H. brunneomaculata*. Bergh described *H. formosa* as having a bladderlike enlarged vagina with longitudinal folds, whereas *H. brunneomaculata* has a narrow vagina and folds are found only in the genital opening through the body wall.

BERGH (1889) described white animals from Mauritius also as *Halgerda formosa*. These animals had yellow ridges

and dark spots. Externally they differed from the 1880 *H. formosa* in basic body color, presence of tubercles, and the absence of a dark band on the tail. At the present time we believe that BERGH's (1889) *H. formosa* is probably a different species.

The name *brunneomaculata* was chosen because of the dark brown spots present on the animal's mantle and body.

DISCUSSION

In the course of preparing this paper we discovered several elements that we feel should be taken into consideration in further work on the *Halgerda*.

A mid-dorsal pattern with four major points of juncture, one in front of the rhinophores and three between rhinophores and branchia, is found in all three animals described in this paper. This configuration is not always clearly seen in *Halgerda brunneomaculata*. The six undescribed species in our collection have the same pattern. For those species that have a color pattern that does not follow the ridges, the major midline points are most obvious in the preserved specimens. In tuberculate species, the major tubercles arise at the points of juncture.

BERGH (1880b) discussed this pattern for *Halgerda tessellata* as did ALLAN (1932) and WILLAN & BRODIE (1989) for *H. aurantiomaculata*. This same pattern appears in other *Halgerda* species, though generally it is not discussed in the text, but appears in the figures or plates accompanying an article. Some examples are found in BERGH (1905:pl. 2, fig. 4a) for *H. elegans* Bergh, 1905; BERGH (1889:pl. 84, fig. 3) for *H. "formosa"*; BERTSCH & JOHNSON (1981:46–47) for *H. terramtuensis*; ELIOT (1904:pl. 34, fig. 1) and GOSLINER (1987:68, fig. 88) for *H. wasinensis* Eliot, 1904; and LIN (1975:pl. 2, fig. 7) for *H. xishaensis* Lin, 1975.

The three new species described in this paper have a very noticeable flange on the inner edge of all but the outermost lateral teeth. BERGH (1880a) also noticed a flange when he described *Halgerda formosa*, as did WILLAN & BRODIE (1989) in their work on *H. aurantiomaculata*. If the presence of the flange is not recognized, it can cause an interpretation of the teeth that gives a far greater angulation than actually occurs.

The three yellowish *Halgerda* (*H. formosa*, *H. tessellata*, and *H. brunneomaculata*) so far described have pectinate outer laterals. This feature is not limited to the yellowish species because it is also found in *H. elegans* Bergh, 1905, and *H. xishaensis* Lin, 1975. What appears to be unique among the yellow forms is the large denticle that occurs on the inner edge of the innermost of the pectinate teeth.

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New Species and Records of *Lepetodrilus* (Vetigastropoda: Lepetodrilidae) from Hydrothermal Vents

by

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Abstract. Two new species of *Lepetodrilus* are described from the east Pacific hydrothermal vents: *L. tevnianus* from the East Pacific Rise near 11°N, where it is associated with the vestimentiferan *Tevnia jerichonana* Jones, 1985, and *L. corrugatus* from the Juan de Fuca Ridge, known from a single specimen, its tentative association being directly on the sulfide chimney. *Lepetodrilus elevatus* McLean, 1988, previously understood to be widely distributed at the east Pacific vents, is confirmed from the Mariana vents, where it apparently lives away from the vestimentiferans with which it is associated in the eastern Pacific. It is the only molluscan species known from both the eastern Pacific and mid-Pacific vents. *Lepetodrilus fucensis* McLean, 1988, previously known from the Explorer and Juan de Fuca Ridges, is reported at the Gorda Ridge. *Lepetodrilus guaymasensis* McLean, 1988, previously known from five specimens, is now known from 127 additional specimens from the type locality.

INTRODUCTION

Lepetodrilus McLean, 1988, family Lepetodrilidae, superfamily Lepetodrilacea, is unique among the genera of archaeogastropod limpets associated with hydrothermal vents in having three pairs of epipodial tentacles and a right cephalic-epipodial penis. Anatomy was described in a companion paper by FRETTER (1988). Relationships of the superfamily have also been discussed by HASZPRUNAR (1988), who assigned it to the suborder Vetigastropoda.

Six species of *Lepetodrilus* were initially described. In this paper I add the descriptions of two more species, and give range extensions or additional records for three of the original species. The new species and records of previously described species add new limits to the expression of morphological character states and new parameters to the understanding of biological associations and the capacity for long distance dispersal in the genus. These topics are treated in the discussion section.

MATERIALS AND METHODS

All specimens reported here were collected by expedition members on various cruises to hydrothermal vent sites that employed the deep-submersible *Alvin* or other submersibles. Limpet specimens were collected with the mechanical arm of the submersible in the course of collecting substrate

samples or general collecting of all organisms. Specimens were preserved on reaching the surface and were originally fixed for 24 hr in 10% formalin-seawater buffered with sodium borate, washed in fresh water, and transferred to 70% ethanol.

Radulae were extracted from preserved specimens after dissolution of tissues with room temperature 10% NaOH for 48 hr, washed in distilled water, dried from a drop of water on a stub having a thin smear of rubber cement, and coated with gold palladium for SEM examination. Repositories of type and other material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum (USNM), and the Museum National d'Histoire Naturelle, Paris (MNHN).

SYSTEMATIC DESCRIPTIONS

Order Archaeogastropoda Thiele, 1925

Suborder Vetigastropoda Salvini-Plawen, 1980

Superfamily LEPETODRILACEA McLean, 1988

Family LEPETODRILIDAE McLean, 1988

Lepetodrilus McLean, 1988

Lepetodrilus McLEAN, 1988:6. Type species: *L. pustulosus* McLean, 1988.

Table 1

Lepetodrilus tevnianus. Measurements and disposition of holotype and paratype specimens.

	Length (mm)	Width (mm)	Height (mm)	Remarks
LACM 2254	9.5	7.9	2.8	Holotype, female (Figures 1–5)
USNM 859484	8.9	7.8	2.8	Intact female
USNM 859484	8.8	7.6	2.7	Intact female
LACM 2255	8.1	7.0	—	Female, shell broken, radula preparation (Figures 7–10)
LACM 2255	6.9	5.8	2.0	Male, shell deformed (Figure 6)

Lepetodrilus species are diagnosed by differences in shell profile, sculpture, penial morphology, and radular morphology, particularly that of the rachidian and first lateral teeth. Each of the previously described species, as well as the two species described here, can be recognized on radular characters alone.

Lepetodrilus tevnianus McLean, sp. nov.

(Figures 1–10)

Description: Shell (Figures 1–3) moderately large for genus (maximum length 9.5 mm). Outline of aperture oval, anterior end markedly tapered to produce faintly angulate anterior tip. Margin of aperture not in same plane, ends raised relative to sides. Anterior slope convex except concave near margin; lateral and posterior slopes concave. Apex at one-quarter shell length from posterior margin, below highest elevation of shell, displaced slightly to right, right side of protoconch remaining visible. Periostracum moderately thick, light yellow-brown, turned in at shell edge. Early shell to 1 mm length devoid of sculpture; single mid-dorsal rib on anterior slope arising first, remaining stronger than all other ribs; fine primary ribs arising at shell length of 1–3 mm; secondary ribs arising at shell length of about 4 mm, quickly assuming strength of primary ribs. Large specimens with 6 ribs/mm at margin. Ribs minutely beaded to correspond to growth lines, remaining strong at later stages of growth. Interior surface glossy, opaque, with scattered white discolorations. Posterior half of shell interior with faintly angulate curved ridge outside of muscle scar. Muscle scar horseshoe-shaped, not deeply marked, positioned on inner surface of curved ridge midway between margin and midline; scar relatively broad, broadest anteriorly, narrow posteriorly. Apical pit prominent, not filled by deposition of callus.

Dimensions of holotype: Length 9.5, width 7.9, height 2.8 mm.

External anatomy (Figures 4–6): Typical for genus. Epipodial tentacles three pairs, one lateral pair and two posterior pairs, each with cylindrical tip and triangular base. Cephalic tentacles long, encircled laterally and ventrally by epipodial folds, eyes lacking. Oral disk broad, mouth Y-shaped. Anterior of foot with double edge, marking opening of pedal gland. Mantle edge with two folds, inner

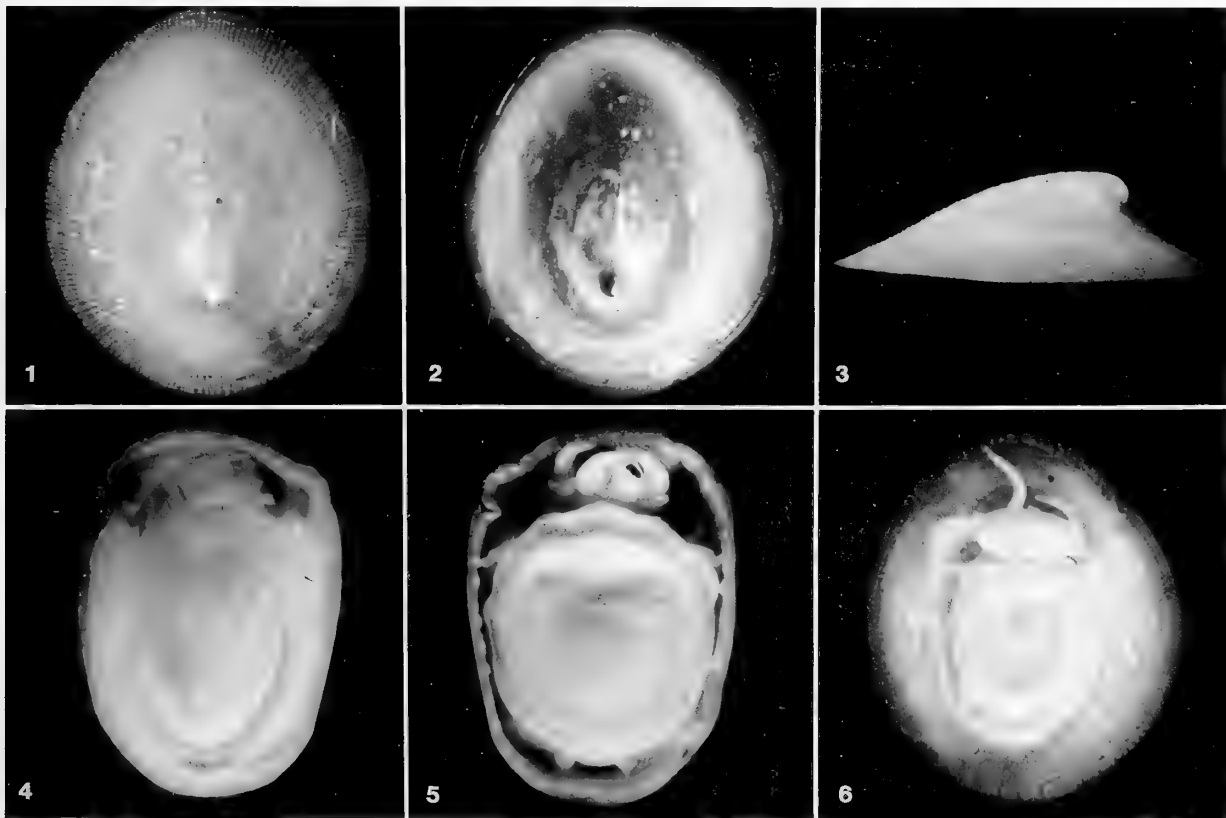
fold smooth to extend under periostracum, edge of outer fold finely divided. Penis of male (Figure 6) flaplike, its origin on right ventral neck. Mantle cavity and ctenidium typical for genus, ctenidium projecting above head in ventral view (Figure 5).

Radula (Figures 7–10): Rhipidoglossate; laterals five pairs, cusp rows of first and second laterals forming inverted-U; marginals numerous, cusp rows descending. Rachidian broad at base, shaft shorter than that of laterals, rachidian with very long, tapered central cusp, edges with about six sharply pointed denticles; shaft of rachidian with projecting lateral extension fitting against edge of first lateral. First lateral large and complex, curved overhang broad at its distal edge. Inner edge of shaft of first lateral continuous with main cusp, projecting so that it appears to be a long pointed denticle like that of rachidian; outer edge of shaft with hooked projection that articulates with shaft of second lateral. Overhanging edge of first lateral with about eight long, unseparated denticles on inner edge, followed by a major denticle and at least three shorter denticles on outer edge. Second, third, and fourth laterals similar to each other, cusps long, tapered, with serrate edges; fifth lateral broader. Marginal teeth similar to each other, tips with numerous, deeply cut serrations.

Type locality: On vestimentiferan *Tevnia jerichonana* Jones, 1985, living on basalt cliff overhanging low temperature venting water, East Pacific Rise near 11°N (10°56.3'N, 103°41.4'W), 2536 m.

Type material: 5 specimens (4 females, 1 male) from the type locality, recovered from washings of specimens of *Tevnia jerichonana*, Alvin dive 1986, 8 March 1988. Received from Cindy Lee Van Dover. Holotype, LACM 2254; 2 paratypes, LACM 2255; 2 paratypes, USNM 859484. Dimensions and disposition of all specimens are given in Table 1.

Remarks: *Lepetodrilus tevnianus* is easily distinguished from the other species of *Lepetodrilus* in characters of the shell, penial morphology, and radula. The shell most resembles that of *L. pustulosus*, but has the strong anterior rib, is broader, has a more angulate anterior (dorsal view), and lacks the diverging curves in the alignment of the beads on the radial ribs, as well as lacking the two supporting



Explanation of Figures 1 to 6

Figures 1–6. *Lepetodrilus tevnianus* McLean, sp. nov. Alvin dive 1982, East Pacific Rise near 11°N, 2536 m. Anterior at top in vertical views. Figures 1–3. Holotype shell, LACM 2254. Length 9.5 mm. Exterior, interior, and left lateral views. Figures 4, 5. Holotype body (female). Dorsal and ventral views. Figure 6. Paratype, male body attached to shell, LACM 2255. Length 6.9 mm.

ridges below the apex on the posterior slope of that species. The flat, non-elbowed morphology of the penis is characteristic. The radula of *L. tevnianus* is unlike that of any other species of *Lepetodrilus*. The rachidian is unique in having a very long cusp and large, conspicuous flanks to the shaft; the first lateral is unique in its prominent inner edge of the shaft.

The significance of the association of this species with a vestimentiferan other than *Riftia pachyptila* is treated further in the discussion section.

Etymology: The name *tevnianus*, means of *Tevnia*, the vestimentiferan on which this species lives.

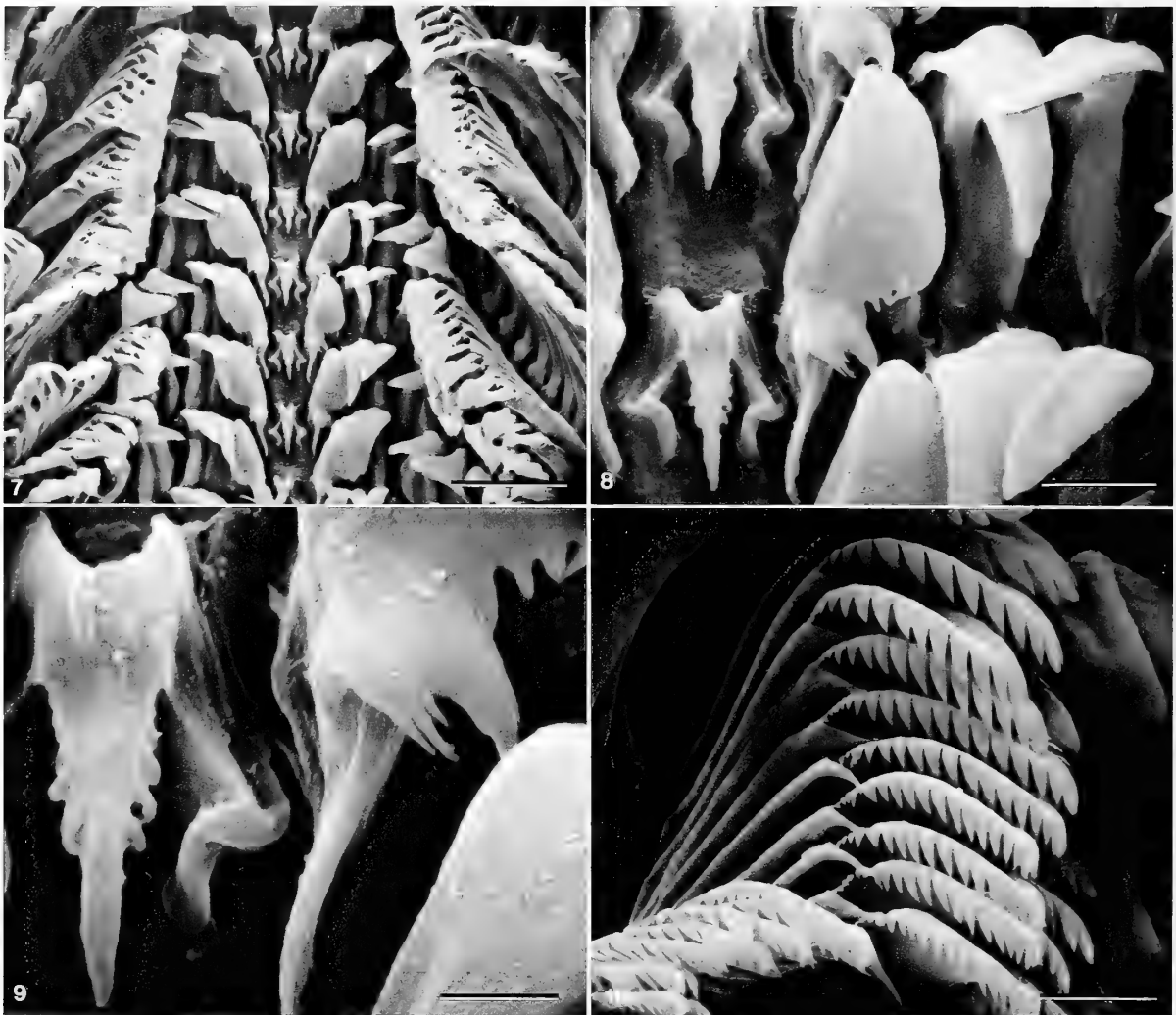
Lepetodrilus corrugatus McLean, sp. nov.

(Figures 11–16)

Description (based on single female specimen): Shell (Figures 11–13) medium-sized for genus (length 6.1 mm). Outline of aperture oval, anterior end slightly narrower than posterior. Margin of aperture not in same plane, ends raised relative to sides. Anterior slope convex, lateral slopes flat, posterior slope convex below apex. Apex at one-eighth

shell length from posterior margin, below highest elevation of shell, apex displaced slightly to right; protoconch surface eroded, not visible on right side. Periostracum moderately thick, light greenish-brown, turned in at shell edge. Early shell to 1 mm length devoid of sculpture. Mature sculpture dominated by about six irregularly formed concentric swellings, producing a wrinkled appearance; additional concentric sculpture of fine growth lines on periostracum. Radial sculpture of low ribs, strongest posteriorly and laterally, interspaces broader than ribs. Ribs only faintly beaded to correspond to growth lines. Interior surface opaque, chalky (probably etched by preservation fluids), showing the coarse, irregular concentric sculpture of the exterior. Posterior half of shell interior with strongly angulate, curved ridge outside of muscle scar. Muscle scar horseshoe-shaped, not deeply marked, positioned on inner surface of curved ridge midway between margin and midline; scar relatively broad, broadest anteriorly, narrow posteriorly. Apical pit prominent, not filled by deposition of callus.

Dimensions of holotype: Length 6.1, width 4.7, height 2.2 mm.



Explanation of Figures 7 to 10

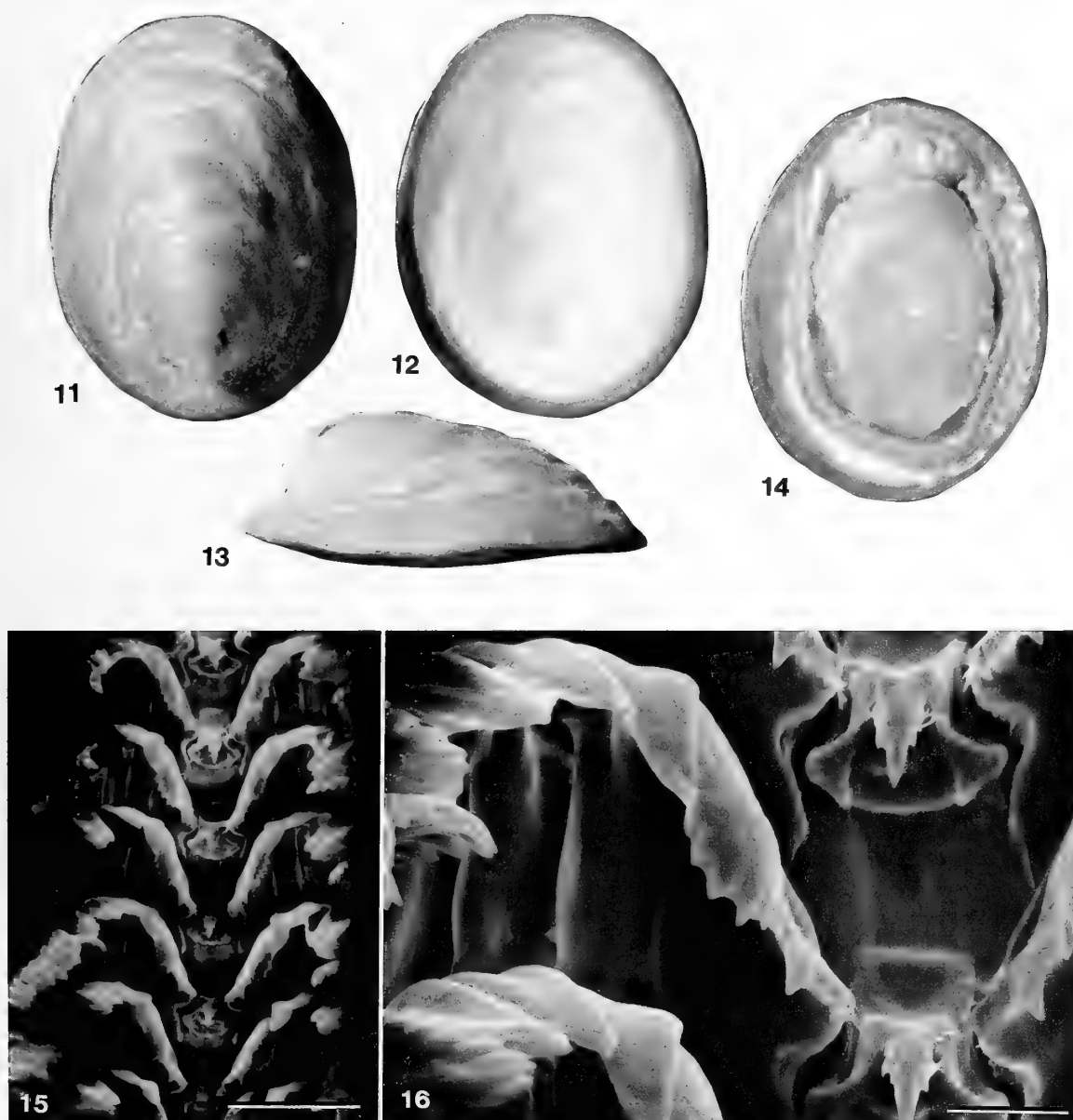
Figures 7–10. *Leptodrilus tevnianus* McLean, sp. nov. SEM views of radula of paratype, LACM 2255. Figure 7. Full width of ribbon. Scale bar = 40 μ m. Figure 8. Rachidian and first three laterals. Scale bar = 10 μ m. Figure 9. Rachidian and adjacent edge of first lateral. Scale bar = 4 μ m. Figure 10. Detail of serrations on marginal teeth. Scale bar = 10 μ m.

External anatomy (Figure 14): Typical for genus. Epipodial tentacles three pairs, one lateral pair and two posterior pairs, each with cylindrical tip and triangular base. Cephalic tentacles short (preserved condition), encircled laterally and ventrally by epipodial folds, eyes lacking. Oral disk broad, mouth Y-shaped. Foot anterior with double edge, marking opening of pedal gland. Mantle edge with two folds, edge of outer fold smooth to extend under periostracum, edge of inner fold finely divided. Mantle cavity and ctenidium typical for genus, ctenidium not projecting above head in ventral view (Figure 14).

Radula (Figures 15, 16): Rhipidoglossate; lateral teeth five pairs, cusp rows of first and second laterals forming inverted-U; marginals numerous, cusp rows descending. Rachidian broad at base, shaft shorter than that of laterals,

with tapered central cusp, edges with about three sharply pointed denticles; shaft of rachidian with projecting lateral extension fitting against edge of first lateral. First lateral large and complex, shaft broad, curved overhang broader distally from rachidian, distal portion bearing about six sharp denticles, inner portion with one major and two or three minor denticles. Second, third, and fourth laterals similar to each other, cusps long, tapered, edges not serrate; fifth lateral with deeply serrate edges. Marginal teeth similar to each other, tips with numerous, deeply cut serrations.

Type locality: Heineken Hollow, Middle Valley, Juan de Fuca Ridge, west of Washington (48°25.8'N, 128°40.9'W), 2420 m.



Explanation of Figures 11 to 16

Figures 11–16. *Lepetodrilus corrugatus* McLean, sp. nov. *Alvin* dive 2252. Middle Valley, Juan de Fuca Ridge off Washington, 2420 m. Anterior at top in vertical views. Figures 11–14. Holotype, LACM 2256. Length 6.1 mm. Exterior, interior, right lateral, and body (female) before detachment from shell. Figures 15, 16. SEM views of radula of holotype. Figure 15. Width of ribbon. Scale bar = 20 μ m. Figure 16. Rachidian and lateral teeth. Scale bar = 10 μ m.

Type material: 1 specimen (female) from the type locality, recovered from sample containing broken pieces of sulfide chimney, *Alvin* dive 2252, 5 August 1990. Recognized during sample sorting by K. Wilson and forwarded by Verena Tunnicliffe. Holotype, LACM 2256. The holotype body is intact except for removal of the radula.

Remarks: *Lepetodrilus corrugatus* is known from a single

female specimen. The morphology of the penis, an important external character in members of this genus, is therefore unknown. Attempts by K. Wilson to locate additional specimens in samples from the Middle Valley site on the Juan de Fuca Ridge have been unsuccessful (V. Tunnicliffe, personal communication). The type locality is a new site on the northern Juan de Fuca Ridge for which there are faunal and structural differences from

other sites that will be described by V. Tunnicliffe. The species is described from a single specimen in order to update knowledge of the family.

Lepetodrilus corrugatus differs from its congeners in both shell and radular characters. It is the only species having the sculpture dominated by deep, irregular concentric undulations. In general proportions and sculpture it is most similar to *L. pustulosus*. Differences, in addition to the corrugate sculpture, are its more oval outline, more posterior apex, coarser radial ribs, and lack of the two strong radial ribs that subtend the apex. It differs from *L. elevatus* in its sculpture and its broader anterior outline, as well as radular characters.

The radula of *Lepetodrilus corrugatus* requires comparison with that of *L. pustulosus* and *L. fucensis*, both of which have similarly proportioned first lateral teeth. The rachidian of *L. corrugatus* differs from that of *L. pustulosus* in having fewer serrations and not having the concave depression on the overhanging surface; details in the placement of cusps of the elongate first lateral also differ. Similar differences separate the radulae of *L. corrugatus* from that of *L. fucensis*; the latter species also differs in having a marked concavity on the overhanging surface of the rachidian.

The occurrence of this species on the sulfide chimney microhabitat is unique in the genus and needs to be verified by the collection of further specimens. It occurs sympatrically with the abundant species *Lepetodrilus fucensis*.

Etymology: The name *corrugatus* is a Latin adjective meaning "wrinkled" or "ridged," with reference to the dominant shell sculpture.

Lepetodrilus elevatus McLean, 1988

(Figures 17–25)

Lepetodrilus elevatus McLEAN, 1988:11, figs. 5,5, 36–44; McLEAN, 1990a:84.

Lepetodrilus cf. *elevatus*: HESSLER & LONSDALE, 1991a:190; HESSLER & LONSDALE, 1991b:171.

New records: 29 specimens from *Alvin* dive 1837, Burke Field vents, Mariana Trough spreading center (18°10.9'N, 144°43.2'E), 3660 m, 28 April 1987. Received from Robert R. Hessler. Disposition: 14 specimens LACM 146884; 10 specimens USNM 882027; 5 specimens MNHN.

Nine specimens from *Alvin* dive 1843, Alice Springs vents, Mariana Trough spreading center (18°12.6'N, 144°42.4'E), 3640 m, 4 May 1987. Received from Robert R. Hessler. Disposition: 5 specimens LACM 146885; 4 specimens USNM 882028.

Remarks: The presence of this species at the Mariana Trough vents has previously been reported by McLEAN (1990a) and by HESSLER & LONSDALE (1991a, b), but detailed commentary and illustrations have not been given. Material from the Mariana Trough (Figures 17–25) matches that illustrated by McLEAN (1988) for specimens

of the typical subspecies *Lepetodrilus elevatus elevatus* from the East Pacific Rise at 21°N. All specimens of the present material have surficial markings on the periostracum made by an unknown organism, but this does not penetrate the periostracum and has no significance for taxonomic comparison. Specimens originally described from the Galapagos Rift were consistently lower in profile (at two-thirds the height of the typical subspecies) and were given the subspecific name *L. elevatus galriftensis*, but the present material has the high profile of the typical subspecies. All specimens of the material from the Mariana Trough appear to be female, none having the broad triangular penis illustrated by McLEAN (1988:pl. 6, fig. 39). The significance of this is unknown and needs to be further investigated. Genetic (electrophoretic) evidence that the two populations represent the same species would also be of interest.

Lepetodrilus guaymasensis McLean, 1988

Lepetodrilus guaymasensis McLEAN, 1988:16, figs. 15, 16, 66–74.

New records: 98 small to medium-sized specimens (not sexed) from *Alvin* dive 1613, Guaymas Basin (27°00.5'N, 111°24.6'W), 2007 m, 5 August 1985. Received from Meredith R. Jones. Disposition: 48 specimens LACM 146886; 30 specimens USNM 882029; 20 specimens MNHN.

Twenty-nine specimens (21 male, 8 female) from *Alvin* dive 1615, Guaymas Basin (27°00.5'N, 111°24.6'W), 2000 m, 7 August 1985. Received from Meredith R. Jones. Disposition: 13 specimens LACM 146887; 10 specimens USNM 882030; 6 specimens MNHN.

Remarks: *Lepetodrilus guaymasensis* was described originally from five specimens; the 127 specimens reported here from the 1985 expedition to the Guaymas Basin (Fred Grassle, Chief Scientist) are a significant increase in the number known. Both samples were recovered from washings of *Riftia pachyptila*.

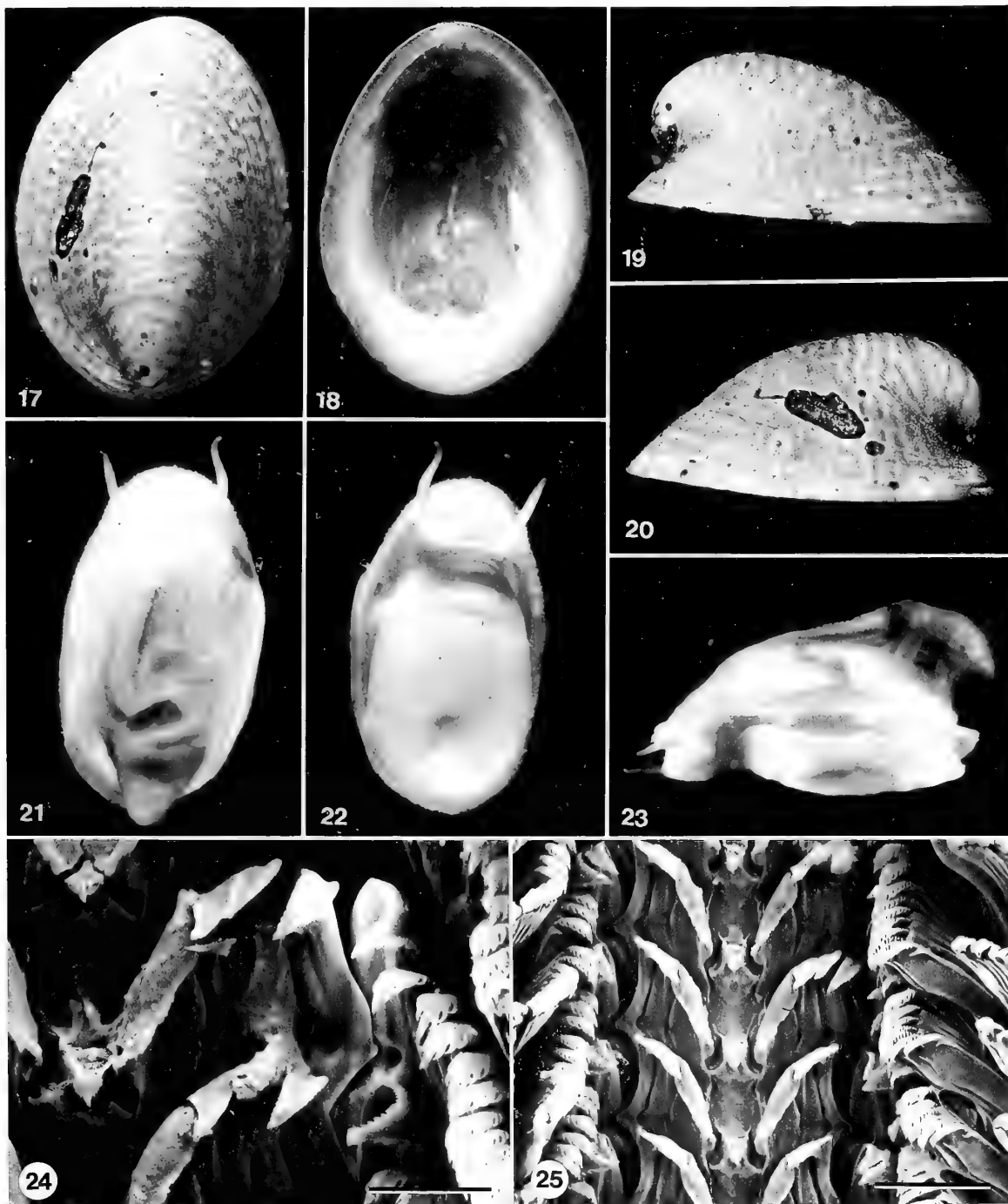
Lepetodrilus fucensis McLean, 1988

Lepetodrilus fucensis McLEAN, 1988:18, figs. 17–20, 75–83; McLEAN, 1990b:496.

New records: 15 specimens (9 male, 6 female) from *Sea Cliff* dive 764, Escanaba Trough, Gorda Ridge (41°00'N, 127°29'W), 3200–3250 m, 3 September 1988. Received from Robert R. Hessler. Disposition: 7 specimens LACM 146888; 5 specimens USNM 882031; 3 specimens MNHN.

Twenty-three specimens (12 male, 11 female) from *Alvin* dive 2036, Escanaba Trough, Gorda Ridge (41°00.4'N, 127°29.3'W), 3240 m, 6 June 1988. Received from Cindy Lee Van Dover. Disposition: 9 specimens LACM 146889; 8 specimens USNM 882032; 6 specimens MNHN.

Remarks: This species, which is abundantly known from the Explorer and Juan de Fuca Ridges, was reported by McLEAN (1990b) from Escanaba Trough on the Gorda Ridge. Disposition of the material is given here. As re-



Explanation of Figures 17 to 25

Figures 17–25. *Lepetodrilus elevatus* McLean, 1988. *Alvin* dive 1837. Burke Field, Mariana vents, 3660 m. Anterior at top in vertical views. Figures 17–20. LACM 146884. Length 6.8 mm. Figures 17–20. Exterior, interior, right, and left lateral views. Markings on shell produced by unknown organism. Figures 21–23. Detached body of same specimen as in Figures 17–20. Dorsal, ventral, and lateral views. Figures 24, 25. SEM views of radula, LACM 146884. Figure 24. Rachidian, lateral, and inner marginal teeth. Scale bar = 20 μ m. Figure 25. Full width of ribbon. Scale bar = 40 μ m.

ported initially, there is no known association with vestimentiferans. A general description of the biotic community of the Escanaba Trough was given by VAN DOVER *et al.* (1990).

DISCUSSION

The description of two additional species brings the total number of described species of *Lepetodrilus* to eight. The genus remains the most speciose of limpet genera in the hydrothermal-vent habitat. Eight of the species are known from eastern Pacific vents; one of these species, *L. elevatus*, is also known from the Mid-Pacific Mariana vents (the only mollusk with such a distribution).

Until now, the only association between species of *Lepetodrilus* and vestimentiferans had been with the vestimentiferan *Riftia pachyptila*. McLEAN (1988) reported that washings of retrieved specimens of that vestimentiferan were highly productive in collecting *L. pustulosus*, *L. elevatus*, *L. ovalis*, and *L. cristatus*. *Lepetodrilus tevnianus* is the only species yet reported to be associated with the vestimentiferan *Tevnia jerichonana*, a vestimentiferan previously reported by JONES (1985) as occurring only at the French expedition site at 13°N. *Lepetodrilus tevnianus* is yet unknown from 13°N, although its vestimentiferan associate is present at that site. *Riftia pachyptila* was not recorded from the type locality of *Tevnia jerichonana* (Alvin dive 1986). The only other *Lepetodrilus* species occurring with *L. tevnianus* was *L. elevatus*. This pattern of distribution suggests that *L. tevnianus* depends on the presence of *Tevnia jerichonana*, and that the most abundant species, *L. elevatus*, can be associated with either species of vestimentiferan, whereas three other species of *Lepetodrilus* are associated only with *Riftia pachyptila*.

The two northernmost occurring species, *Lepetodrilus fucensis*, which occurs clustered on hard surfaces near vents and chimneys, and *L. corrugatus*, which is now known from a single specimen, but may prove to be associated with the hard surface deposits of sulfide chimneys, differ from other eastern Pacific species in having no known association with vestimentiferans. The physical and biological parameters of the sulfide chimney habitat have been discussed by TUNNICLIFFE (1990), although the limpets were not mentioned.

Lepetodrilus elevatus, the most broadly distributed species of the genus, is also the most diverse in its substrate associations. At the eastern Pacific vents it occurs with two different species of vestimentiferans, yet it appears to be capable of living away from vestimentiferans, there being no reported vestimentiferans at the Mariana Trough.

HESSLER & LONSDALE (1991a, b) have recently discussed the biogeographic implications of the species known from the Mariana Trough and the eastern Pacific. The fact that one species of *Lepetodrilus* has bridged the gap seems difficult to explain. However, HESSLER & LONSDALE (1991) noted that "two now-extinct portions of the mid-

ocean ridge system would have allowed comparatively easy interchange 43 and 55 million years ago."

In the genus *Lepetodrilus* the biogeographic affinity between the East Pacific Rise and the Juan de Fuca Ridge extends only to the generic level, as no species are shared between the two systems. Biogeographic affinity of these two systems has been treated by TUNNICLIFFE (1988).

My earlier assessment (McLEAN, 1988) that the lepetodrilaceans may represent limpet derivatives of unknown Paleozoic or Mesozoic archaeogastropods has not been challenged nor supported with further evidence. Additional arguments in support of the concept that the hydrothermal-vent fauna as a whole represents an ancient relict fauna have been given by TUNNICLIFFE (1991; in press). A concerted effort to apply the techniques of molecular genetics will be necessary to test this hypothesis of antiquity, but that is left to future investigators.

ACKNOWLEDGMENTS

For providing material of the new species and new records reported here I thank: Cindy Lee Van Dover of Woods Hole Oceanographic Institution; Verena Tunnicliffe and K. Wilson of the University of Victoria, British Columbia; Bob Hessler and Michel Boudrias of Scripps Institution of Oceanography, Fred Grassle and Rosemarie Petrecca of Rutgers University, New Jersey; and Meredith Jones of the U.S. National Museum of Natural History. Photographs are the work of Bertram C. Draper. SEM work was done by C. Clifton Coney, using the CEMMA facility of the University of Southern California. For helpful commentary I thank Anders Warén of the Swedish Museum of Natural History, Stockholm, and two anonymous reviewers.

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A Defensive Value of the Thickened Periostracum in the Mytiloidea

by

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Abstract. Laboratory experiments demonstrate the advantages which accrue to epifaunal mussels from their possession of a thick periostracum, as a defense against boring predation. Muricid gastropods, *Nucella lapillus* and *Morula musiva*, displayed a statistically significant preference for boring those valves from which the thick periostracal layer had been removed. Although it is possible for muricids to penetrate the periostracum it is suggested that this tough, relatively inert, layer is more difficult to penetrate than the calcareous parts of the shell. In this respect its defensive value is analogous to that of the intra-shell layers of conchiolin reported in certain oysters and Corbuloidea. The thickness of the earlier formed periostracum diminishes as the individual ages, either by decay or abrasion, and in most cases it is thinnest, or even absent, over the oldest parts of the shell. This may have some bearing on the position of most boring activity. As yet it is unclear whether the thickening of the mytilacean periostracum was selected for by the evolution of boring predators or whether the defensive value was a fortuitous spin off of a non-adaptive or otherwise selected character.

INTRODUCTION

The primary function of the molluscan periostracum is considered to be one of involvement in shell secretion, either as a template onto which the calcareous portion of the shell forms (TAYLOR & KENNEDY, 1969) or as a barrier partitioning the extrapallial fluid from the poisoning effects of magnesium ions in seawater and contamination by sediment particles (CLARK, 1976). The sheet may also protect the calcareous shell from dissolution in acidic waters; hence its extreme development in some freshwater taxa (TEVESZ & CARTER, 1980). More recently, some authors have suggested that the periostracum of some mollusks may have a defensive rôle. WRIGHT & FRANCIS (1984) have experimentally shown that the periostracal awns of *Modiolus modiolus* (Linnaeus, 1758) inhibit pedal attachment of the boring muricid *Nucella lapillus* (Linnaeus, 1758) from which they infer a defensive value. BOTTJER (1981) examined the shells of the cymatiid gastropod *Fusitriton oregonensis* (Redfield, 1846), finding that areas of the shell where the thick hairy periostracum was intact showed

fewer borings and encrusting epibionts than regions where the periostracum had been removed by erosion. This paper considers further the defensive value of the mytilid periostracum in the deterrence of boring muricid predators.

The Mytiloidea possess a particularly thick periostracum which, despite the ravages of decay and abrasion, is remarkably persistent through life. Although there is intra-specific variation in the value, initial measurements for 29 species of byssate mytilaceans show that the intact layer always exceeds 20 μm in thickness (Harper, unpublished). The highest value recorded is for an individual of *Choromytilus chorus* at over 400 μm , but for the vast number of species the value lies between 20 and 80 μm (example values include *Perna viridis* (Linnaeus, 1758), 45 μm ; *Septifer virgatus* (Wiegmann, 1837), 59 μm ; and *Mytilus edulis* (Linnaeus, 1758), showing a wide variation up to 70 μm). These high values contrast directly with those for a number of other epifaunal bivalves, for example oysters and pectinids, which have extremely thin periostraca (less than a micron thick), which is seldom detectable beyond the valve margin. Muricid gastropods are well known for their abil-

ity to feed on epifaunal bivalves by boring through the prey shell to gain access to the flesh beneath. Indeed muricids are considered a particularly serious menace to epifaunal bivalves (GALTSOFF, 1964). Boring is effected by a largely chemical means by way of a cocktail of acids, enzymes, and chelators delivered by the accessory boring organ (ABO) located in the foot and is assisted by the rasping action of the radula (reviewed by CARRIKER, 1981). What effect does the thick mytilacean periostracum have on the actions of these boring gastropods?

EXPERIMENTAL INVESTIGATION

Simple choice experiments were designed to test the relative susceptibility of mussels with and without a thick periostracum to boring muricid attack. Predators were offered the choice of prey with one valve possessing an intact periostracum and the other from which the periostracum had been removed. Dogwhelks are known to display marked preferences for borehole site and that this preference is learned, such that an individual may show gradual improvement in accuracy of borehole siting with experience (HUGHES & DUNKIN, 1984). In view of this it was considered inappropriate to test the hypothesis by using shaved regions of the same valve. By using whole valves to represent the choices it was hoped to nullify the effects of individual preferences for boring various parts of the valve, lest these preferences overrode the presence or absence of the periostracum. These experiments were carried out by E.M.H. at Dunstaffnage Marine Laboratory, Oban (Scotland) during May and October 1991 and the Swire Marine Laboratory, Hong Kong during July 1991.

Scottish Experiments

Small individuals of *Mytilus edulis* (Linnaeus, 1758), 7–20 mm, were collected from the intertidal zone of Dunstaffnage Bay, Oban (grid reference NM 886340). Potential prey were selected which were free from marginal damage and adherent epibionts, and which also appeared to possess a complete periostracal cover. One valve of each individual, either left or right, was then shaved with a scalpel blade to remove all the periostracal sheet, thus exposing the calcareous shell below. Individuals of *Nucella lapillus* were collected from the small bay east of Camas Rubha na Liathaig, close to Dunstaffnage Bay (grid reference NM 878344), where they were observed feeding on both mussels and barnacles. No size selection of the predators was made. Five experiments were run in outdoor tanks supplied with flowing natural seawater, running to waste. The water temperature ranged between 12°C and 13°C. Approximately 100 mussels were used in each tank and the relative proportion of left and right shaved valves was noted (see Results). Individuals were randomly scattered and allowed to attach singly on both the floor and sides of the tank. Formation of aggregates was discouraged.

Two days elapsed before introduction of the predators. This delay had two purposes; firstly, to allow the mussels to adopt their natural orthothetic position (with commissure perpendicular to the substratum), thus exposing both valves equally to the predators and secondly, to allow the newly exposed shell surfaces to acquire an adsorbed coating of metabolic products from the mussels. CARRIKER & VAN ZANDT (1972) discovered that the muricid *Urosalpinx cinerea* (Say) was attracted to the shells of the oyster *Crassostrea virginica* Gmelin, 1789, by material adsorbed onto the exterior of the shell. It was, therefore, important that the action of shaving the valves did not remove these cues, making the shaved valve less attractive. Although we do not know whether two days is sufficient to acquire a reasonable “biofilm” it is likely that there would be some reparation within this time. After this rest period, 30–40 dogwhelks were introduced to each tank.

Frequent observations were made on the feeding behavior of the muricids and the defensive behavior of the mussels. All eaten bivalves were retrieved and the following information recorded: valve height, method of attack, whether the attack was on the left or right valve, the position of any boreholes, and whether they passed through the periostracum or not. The same information was recorded for any failed boreholes on these and the surviving mussels. Each trial lasted 15–20 days.

Hong Kong Experiments

In Hong Kong a single experiment was run with the methods and experimental set up being essentially as above. Small individuals (up to 30 mm) of the green lipped mussel *Perna viridis* were obtained from the intertidal zone at Wu Kwai Sha (New Territories). Predatory *Morula musiva* (Kiener, 1835) were collected on the shore at Cape d'Aguilar (Hong Kong Island). *Morula musiva* appears to be an experienced predator of mussels, having been observed boring *Perna* and *Brachidontes variabilis* (Krauss, 1848) on the shores at Wu Kwai Sha, while members of the Cape d'Aguilar population bored *Septifer virgatus* and *Hormomya mutabilis* (Gould, 1861) in aquaria. Seawater temperatures during the investigation fluctuated between 30°C and 32°C.

Survey of Periostracal Thickness

Many of the mussels available at the chosen localities had incomplete periostraca. In order to survey the changes in periostracal thickness across the valve, 10 individuals of 20 mm *Mytilus edulis*, with apparently intact periostraca, were collected from Dunstaffnage Bay (Oban). Sections along the maximum growth direction were made from the valves which had been set into resin blocks to prevent the periostracum spalling off during sawing. Cut surfaces were then polished and etched slightly. Traverses were made along the section using scanning electron microscopy and

Table 1

Experimental results of choice trials involving muricids and mytilids. The null hypothesis used states that there is no preference between boring valves with or without a periostracal covering. Analysis by χ^2 one-sample test: — = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Predator and prey	λ	Total number bored	Number in shaved valves (left, right)	Number in intact valves (left, right)	P
<i>Nucella lapillus</i> vs. <i>Mytilus edulis</i>	1	55	40	15	**
"	2	26	(15, 25) 18	(7, 8) 8	—
"	3	32	(5, 13) 26	(4, 4) 6	***
"	4	55	(13, 13) 43	(2, 4) 12	***
"	5	27	(15, 28) 22	(8, 4) 5	***
"			(11, 11)	(3, 2)	
<i>Morula musiva</i> vs. <i>Perna viridis</i>		26	19	7	*
			(9, 100)	(1, 6)	

changes in thickness of both periostracum and shell recorded.

RESULTS AND ANALYSIS

Both *Mytilus edulis* and *Perna viridis* were readily preyed upon by the muricid gastropods. The vast majority of recorded attacks were boreholes through a single valve, although a small number (11%) of *Mytilus* were edge-bored, damaging both valves. These edge-bored victims were excluded from the statistical analysis, as were the small number of *Perna* which were taken with no apparent valve damage. Table 1 records the relative number of successful boreholes through both intact and shaved valves. In all experiments the number of complete boreholes sustained by the shaved valves exceeded that of those with a continuous periostracal cover.

The positions of completed borings in *Perna* and in one of the *Mytilus* experiments are shown in Figure 1. Although boreholes were recorded from most regions of the valves it is clear that the majority are located in the posteriodorsal position, although many are also sited close against the valve margins.

Recognizable failed boreholes were infrequent (*Mytilus*, $n = 8$, and *Perna*, $n = 4$). This is presumably because of the artificial conditions employed here and also because of the problems of identifying boreholes abandoned during the very earliest stages. Active defense by the prey was observed including valve flapping and flailing of the foot as observed by WAYNE (1987), while intraspecific aggression was displayed by individuals of *Nucella lapillus* along

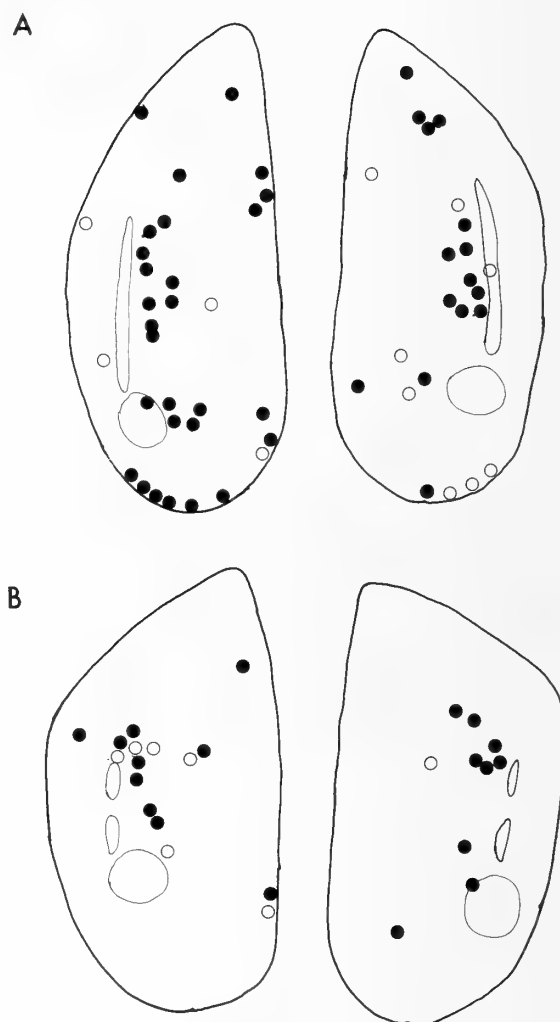


Figure 1

Positions of boreholes. A. *Mytilus edulis* bored by *Nucella lapillus* (experiment 4) in Table 1. B. *Perna viridis* bored by *Morula musiva*. Closed circles indicate bores made in the shaved valves and open circles those in unshaved valves.

with interloping behavior as described by HUGHES & DUNKIN (1984).

Analysis

Since the epibyssate mytilids are eivalve, the areas of both the shaved and intact valves are equal, and since they adopt an orthothetic life position, both valves are equally exposed to predation. Although SEED (1969) has proposed that dextrally coiled muricids are likely to prefer to bore the right valves of mussel prey there has been no statistical evidence to verify this for smaller mussels (e.g., WICKENS & GRIFFITHS, 1985; BUYANOVSKY, 1992), although Buyanovsky does suggest that there is a preference for the right valve in mussels in the size class 20–34.9 mm. Analysis of

Table 2

Data showing the original ratio of mussels with shaved left and right valves and the ratio in which these were bored. The null hypothesis used states that there was no preference for boring right or left valves. Analysis by χ^2 one-sample test fails to reject this null hypothesis.

Predator and prey	Original ratio of left and right shaved valves	Ratio of attacks on left and right shaved valves	χ^2
<i>Nucella lapillus</i> vs. <i>Mytilus edulis</i>	63:59	22:33	2.98
	34:76	9:17	0.17
	43:75	15:17	1.5
	61:94	23:32	0.14
	40:53	14:13	0.87
<i>Morula musiva</i> vs. <i>Perna viridis</i>	43:68	10:16	0.001

the data from these experiments (Table 2), using a χ^2 one-sample test fails to reject the null hypothesis (at the 5% level) that shaved right and left valves are bored in the same proportions as their relative abundance in the tank (*i.e.*, their encounter rate). Therefore, if the presence or absence of periostracum is of no consequence to the actions of a boring muricid we might expect boreholes to be equally distributed between the shaved and intact valves (the null hypothesis). Table 1 shows that in each experiment most boreholes were located on the shaved valve. Analysis by a χ^2 one-sample test rejects the null hypothesis for five out of the six trials at the 5% level of significance. In only one of the experiments, that with the smallest data set ($n = 26$), is there a failure to reject the null hypothesis at the

5% level. Further analysis using a 2×2 contingency table (right and left valves versus shaved and unshaved valves) for each of the data sets prove non-significant ($P > 0.05$) for any side on the preference for shaved and unshaved valves. There is, therefore, a statistically significant preference for boring the valve without a periostracum. It is interesting to note that in the small number of cases where the valve margins of both valves were bored the hole was asymmetric, being more developed on the shaved valve. This situation did not necessarily correspond with the muricids sitting on that side of the shell.

The distribution of periostracum over the entire valve surface of *Mytilus edulis* was recorded for 10 individuals in which the layer was apparently intact. Table 3 shows the recorded thicknesses at two key points for each of the studied individuals; the valve margins and the area above the digestive gland. There is a considerable amount of variation in initial periostracal thickness among individuals, as measured where it lips over the valve edge. Values ranged between 20 and 70 μm , and similar variation has been observed in mussels from other localities. The cause and possible adaptive significance of this variation is as yet unclear. The periostracum of *Mytilus edulis* is characterized by its tripartite structure with a vacuous central layer being flanked by apparently solid layers (DUNACHIE, 1963). This well-defined structure allows easy recognition of incomplete periostracum; well worn areas frequently show that the outer and middle layers are missing, or partially complete. Not surprisingly, in each of the traverses periostracal thickness diminished towards the umbo region, although the decline was not necessarily gradual and progressive. In some cases distinct patches were thinned surrounded by more pristine areas. Eight of the 10 individuals possessed less than 10 μm cover on the older parts of the shell.

DISCUSSION

Drilling muricids are capable of penetrating mussel periostracum (see also CARRIKER, 1978), but there is a definite preference for boring mussels without the layer. There are two possible implications of this apparent preference; either the presence of the periostracum in some way inhibits the boring action, or the denuded surface is favored as a resting site for the gastropod while boring. Of these two options we favor the former. Although it has been suggested that some muricids do show positive thigmotaxis there is no evidence here that these gastropods were showing this preference. The shaved valves were in many cases actually smoother than the those with periostracal cover, in particular those which had become worn so as to expose the central vacuous layer of the sheet.

How then does the presence of a thick periostracum inhibit boring? Removal of the periostracal layer is not likely to make the bivalve more vulnerable because of the overall decrease in valve thickness: not only is this decrease negligible (for a 20 mm *Mytilus* removal of the periostra-

Table 3

Periostracal thickness recorded at key points on the shell of each of 10 individuals of *Mytilus edulis* collected from Dunstaffnage Bay, Oban (Scotland).

Individual	Thickness in digestive gland region (μm)	Thickness at valve margin (μm)
1	65	70
2	11	30
3	9	23*
4	11	20
5	8	20
6	21	12*
7	8	17*
8	4	17*
9	10	19*
10	0	12*

* Denotes areas at the valve margin where the periostracum is already eroded, exposing the central vacuous layer.

cum only reduces the thickness of the most frequently attacked part of the shell by perhaps only 1–2%) but also there is no evidence that gastropods have any mechanism for gauging prey shell thickness (KABAT, 1990).

GABRIEL (1981) tested the susceptibility of various shell microstructures to destruction by abrasion and acidic and enzymic attack, in mimicry of gastropod boring. Unfortunately she did not test the ability of the periostracum to resist components of the ABO secretion. The periostracum contains a sclerotized tanned protein which is chemically fairly inert and durable (SALEUDDIN & PETIT, 1983). These features may make the sheet less vulnerable to the ABO secretions than other organic material in the shell. The structure of the intact periostracum is very dense and this may impede penetration by ABO secretions; indeed CARRIKER (1978) notes that the chemical dissolution of the periostracum is accelerated on damaged areas. Additionally, the tanned nature of the periostracum imparts a degree of hardness which may impede action of the radula. TAYLOR & LAYMAN (1972) measured the physical properties of most bivalve shell microstructures, including microhardness. However, they restricted their survey to calcareous parts of the shell and therefore did not tackle the periostracum. Preliminary studies suggest that the brittleness of the mussel periostracum does not readily lend itself to determining accurately microhardness.

Additionally, in *Mytilus edulis* the three-layered structure of the periostracum, with its central vacuolated layer, may inhibit the boring action by yielding under radular pressure, so preventing the radula teeth from penetrating the dense outer layer (acting in a manner similar to foam packing). However, this hypothesis remains to be tested.

TAYLOR (1990) demonstrates that *Morula musiva* and *Thais clavigera* Kuster, 1858, are frequently thwarted in their attempts to bore the mangrove oyster *Saccostrea cucullata* (Born, 1778) by the conchiolin layers within the prey shell. Failed boreholes frequently terminate at these layers and those borings which do penetrate them are often of reduced diameter at that point. In the field he discovered that most actively boring muricids were in the act of penetrating the conchiolin when disturbed. The implication of these observations are that the conchiolin sheets, which are of similar composition to molluscan periostracum, are more difficult to bore through than the foliated calcite. This additional protection is particularly valuable in these oysters as their shell structures have been shown by GABRIEL (1981) to be the most susceptible of all molluscan shell structures. Various other authors, for example LEWY & SAMTLEBEN (1978), have suggested that members of the infaunal genus *Corbula* derives similar benefit in defence against naticid gastropods from its intra-shell conchiolin sheets.

We have no evidence that boreholes started in valves with periostracum are often abandoned; indeed as noted the number of failed boreholes was small (however, it should be noted that boreholes may be abandoned at a stage before they are readily perceived). It would, there-

fore, seem that the presence of periostracum deters commencement of boring rather than decreasing the likelihood of success once started. Both *Nucella* and *Morula* spend long periods of time inspecting potential prey items before boring; HUGHES & DUNKIN (1984) estimate 1–2 hours for the former. The implication is that the muricids are capable of selecting areas of absent or thin periostracum before feeding begins. It is now well known that dogwhelks feed optimally (BURROWS & HUGHES, 1990; HUGHES & BURROWS, 1990) and are capable of making economic “decisions” balancing energy gain from a particular prey choice against energy and time expended in obtaining it.

Boring is a time consuming process, each meal taking several days to complete. In the natural environment failure to complete a borehole may result from adverse environmental conditions, for example desiccation during low tide, attack by a predator, or displacement by a competitor. In these experiments the participants were not exposed to a tide or other predators. It should also be noted that several of the failed boreholes occurred on specimens with completed holes and that in these instances two gastropods were observed simultaneously boring the same prey item. In this case failure to complete the bore results from one gastropod reaching the flesh before the other, rather than any other reason.

Many studies have revealed a pronounced stereotypy in borehole positioning and the distribution recorded here parallels that noted by HUGHES & DUNKIN (1984) for *Nucella* boring in *Mytilus* both in the laboratory and the field, and TONG (1987) for *Morula* boring *Brachidontes variabilis*. Our laboratory observations show that *Morula* also utilized the same position when boring other mytilids *Septifer virgatus* and *Hormomya mutabilis*. A number of different hypotheses have been advanced to explain this preference for the older parts of the shell. GRIFFITHS (1981) postulates that the narrower part of the mytilid shell may be easier to grip, but this explanation is probably only reasonable in a consideration of naticid predation rather than for muricids which do not hold the prey in the foot while boring. HUGHES & DUNKIN (1984) suggest that this position gives rapid access to the digestive gland, the most calorifically rewarding part of the flesh, and that the more experienced the dogwhelk, the more accurately the borehole is located. In these experiments we found that often the muricids failed to consume the entire prey, leaving residual mantle and foot tissue behind, again implying that consumption of the the digestive gland and other viscera is favored. HUGHES & DUNKIN (1984) also made the puzzling assertion that this preferred boring site also corresponds to the thinner parts of the shell. Evidence from the traverse study shows a gradual thickening of the shell away from the valve edge. This is in accordance with the bivalve mode of growth whereby shell material is continuously added by the entire surface of the outer mantle fold. One would anticipate that the pronounced tendency to bore through the older parts of the shell would seem to penetrate the thicker shell, except in very high energy environments

where the shell may be very badly abraded. However, periostracum is subject to thickness diminution by the agencies of fungal and bacterial decay, rasping of grazing animals, and abiotic erosion. In many bivalves, particularly those with thinner periostraca, the extent of the periostracal layer is restricted to the more newly formed parts of the shell. Indeed even in many mytilids examined the periostracum is absent over much of the older part of the shell, and this study shows that even those individuals with apparently intact periostraca show substantial thinning over that area. It might be argued that by boring over the posteriodorsal region of the shell the gastropods are not only gaining from direct access to the more lucrative digestive gland but also from the advantage of boring in an area with little or no periostracal cover.

ANSELL (1969) describes bivalve defenses as either active or passive. Deterrence of boring predation by the possession of a thick periostracum falls into the latter category. Undoubtedly the mussels also gain defense against these and other predators by their tendency to clump (OKUMARA, 1986; LIN, 1991) and also by the more active mechanisms described by WAYNE (1987) and PETRAITIS (1987). Periostracum is a non-renewable defense and its value will wane with increased wear, but by the time it has completely worn away the mussels are likely to have reached a size refuge from their boring predators. This is especially true for the rapidly growing *Perna viridis* (SEED, 1990).

It is tempting to speculate that other epifaunal bivalves with thick periostraca (e.g., members of the Arcacea) derive a similar benefit against boring muricids and that those infaunal bivalves also possessing this feature may be likewise defended from attack by naticid gastropods. CLARK (1976) suggests that the extreme thickness of the mytilacean periostracum is likely to be a derived feature. It would be interesting to determine whether this character resulted from selection pressure exerted by boring predators or whether thickening preceded their evolution and that the defensive value was merely fortuitous. The first boreholes attributable to the muricids occur in rocks of Lower Cretaceous (Albian) age (TAYLOR *et al.*, 1983). As yet we have very little evidence of fossil periostracum; the layer seldom survives the life time of the mollusk let alone taphonomic processes. However, HUDSON (1968) does recognize a structure on the outer surface of the Jurassic mytilid *Praemytilus strathairdensis* (Anderson & Cox, 1948) which he interprets as periostracum. Hudson measured this putative periostracum as having a maximum thickness of 15 μm . Such a value, although thicker than that recorded for many bivalves (Harper, unpublished), is rather lower than has been recorded for Recent epibyssate Mytilacea. At present we can only speculate on the significance of this datum. One possibility is that a slight relative thickening of the periostracum in earlier mussels may have been associated with their tolerance to hyposaline waters analogous to the condition found in many freshwater taxa (TEVESZ & CARTER, 1980); Hudson interprets the beds in which *Praemytilus* is found as having been deposited in brackish la-

goons. If confirmed in other pre-Cretaceous mytilids periostracal thickening would thus have been preadaptive for inhibition of boring by muricids, although this additional selection pressure may well have led to yet further thickening thereafter. Yet we have no way of telling whether these specimens of *Praemytilus* possessed fully intact periostraca nor any comparative data for other Jurassic mytilids. Further evidence from palaeontological material is required to resolve the question of the primary cause for thickening of the periostracum in these bivalves.

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Morphological and Allozyme Variation in *Littorina sitkana* and Related *Littorina* Species from the Northeastern Pacific

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Abstract. We studied the morphological and biochemical systematics of some *Littorina* with direct development from the northeastern Pacific. We describe differences in geographic distribution, body pigmentation, size at first reproduction, shell morphology, and behavior between *L. sp.* and its close relative *L. "kurila."* We also discuss field characters useful in distinguishing *L. sp.* from *L. sitkana* Philippi, as these two species often have an overlapping distribution on northeastern Pacific shores of intermediate exposure. The systematics of these gastropods are difficult because there is considerable within-species variation in shell morphology. There was more variation in shell shape within split broods of *L. sp.* grown at high and low growth rates than was seen among three different taxa collected in the field. Even shell ornamentation was not always diagnostic; offspring of heavily ridged *L. sitkana* parents were completely smooth when cultured at high growth rates.

Littorina sitkana and *L. sp.* from areas of intermediate wave exposure on Tatoosh Island, Washington, did not hybridize. The two populations were fixed or nearly fixed for different allelic allozymes at the Pep-3, Gpi-1, Sdh-4, and Pgm-1 loci and had distinctive esterase banding patterns. This agrees with our conclusions from our morphological and hybridization studies that *L. sitkana* and *L. sp.* are separate species. Our electrophoresis results suggested that *L. sp.* was closely related to *L. subrotundata* (Carpenter); however, the two taxa had fixed differences at the Pep-3 locus. We estimated a preliminary phylogeny based on allozyme data for these northeastern Pacific *Littorina* and for *L. saxatilis*, *L. obtusata*, and *L. littorea* from the northwestern Atlantic.

INTRODUCTION

Gastropods of the genus *Littorina* (*sensu* REID, 1989) inhabit the intertidal zone on rocky shores over much of the north temperate zone. They have been the subjects of numerous studies contributing to intertidal ecology and population genetics (see reviews by RAFFAELLI, 1982; BERGER,

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1983; FALLER-FRITSCH & EMSON, 1985; JANSON, 1987). The results of such studies will be misleading if, unknown to the investigator, the populations being studied contain a mixture of species. As a result of recent systematic work in Britain, *Littorina saxatilis* (Olivi, 1792) has been split into three to four species and *Littorina obtusata* (Linnaeus, 1758) has been split into two species (reviews by FRETTER & GRAHAM, 1980; JOHANNESSON & JOHANNESSON, 1990; RAFFAELLI, 1990; REID, 1990; WARD, 1990).

Recent work has helped clarify the status of oviparous, direct-developing littorinid species from the northern Pacific (BOULDING, 1990a, b; REID, 1990; REID & GOLIKOV, 1991; REID *et al.*, 1991). BOULDING (1990a) mentioned *Littorina* sp., a new subspecies of *Littorina kurila* Middendorff that was related to *Littorina sitkana* Philippi and lived on Tatoosh Island and other wave-exposed shores in the northeastern Pacific. The morphological similarity between *L. sp.* from Tatoosh Island and *L. kurila* Middendorff from Adak Island had been initially recognized by Reid (D. G. Reid in lit. to E. G. Boulding). REID (1990, note added in proof) examined the syntypes of *L. kurila* Middendorff and found the pallial oviducts were of the form found in *L. sitkana*. He suggested that *L. kurila* Middendorff was a junior synonym of *L. sitkana* Philippi and that a new name might be necessary for the species he referred to as *L. "kurila."* Reid included both specimens from Adak Island in the Aleutians and specimens from Tatoosh Island in *L. "kurila."* In her thesis BOULDING (1990b) considered the Tatoosh Island form to be a taxon separate from the Adak Island form. She discussed the morphological and allozyme characters distinguishing these two taxa from each other and from *L. sitkana*. REID & GOLIKOV (1991) have suggested that *L. sp.* and *L. "kurila"* (*sensu* BOULDING, 1990b) be included in the taxon *L. subrotundata* (Carpenter, 1864) because they found no differences in the pallial oviducts of these three taxa.

The above illustrates that the systematics of *Littorina* are difficult, especially if based only on shell morphology, because the degree of morphological variation within species is large relative to the variation between species. In general, measurement of gastropod shells is challenging because there are few homologous points (BOOKSTEIN *et al.*, 1985; A. J. Kohn, personal communication). The parameters used by Raup to model shell shape (RAUP, 1961, 1966) are difficult to measure on an intact shell (KOHN & RIGGS, 1975; Schindel, unpublished manuscript). Nevertheless, it is worthwhile to attempt to separate species with similar morphology on the basis of their shell characters because such characters can be measured on recovered shells, on museum specimens, and on fossils, and because they were used exclusively in the early species descriptions of these littorinids (PHILIPPI, 1846; MIDDENDORFF, 1848; CARPENTER, 1864; DALL, 1921; OLDROYD, 1927; PALMER, 1958). Previous workers working on closely related species of *Littorina* have used discriminant analysis and principal component analysis to look for morphological separation of different groups (MURRAY, 1982; WELLINGTON & KURIS,

1983; JANSON & SUNDBERG, 1983; JANSON, 1985; JANSON & WARD, 1985). With these methods the information in a number of morphometric variables can often be reduced to two or three composite variables that summarize most of the information and differentiate between the groups better than any two or three morphometric variables could do alone (REYMENT *et al.*, 1984).

That shell morphology of gastropods varies with environmental conditions has long been known (COLTON, 1922; CROTHERS, 1971; VERMEIJ, 1980). The shell shape of *Littorina littorea* Linnaeus, 1758, has been shown to change dramatically with growth rate (KEMP & BERTNESS, 1984). Shell morphology has been shown to change with proximity to crabs preying on conspecific gastropods (APPLETON & PALMER, 1988; PALMER, 1990). This plasticity in shell form leads to problems of species determination when snails from different locations are compared because the observed morphological differences might have a genetic component or they might be caused solely by environmental differences among the different locations. To investigate the genetic basis of morphological differences in shell morphology we raised the offspring of parents collected from various field sites in a "common garden" and compared the morphology of these offspring; this procedure is rare in the zoological literature.

Another method of distinguishing morphologically similar species is protein electrophoresis. Electrophoresis has been frequently used to separate morphologically similar but reproductively isolated species complexes; if two sympatric taxa are shown to be fixed for different alleles at a locus of the same allozyme, the two taxa must be reproductively isolated (FERGUSON, 1980; BUTH, 1984).

Allozyme electrophoresis has been used to clarify the status of sibling species pairs such as *Littorina saxatilis* (Olivi) and *Littorina arcana* Hannaford Ellis, 1978 (WARD & WARWICK, 1980; WARD & JANSON, 1985; KNIGHT & WARD, 1991). The latter two species are particularly interesting because their shell morphology is almost identical (HANNAFORD ELLIS, 1979) and there are no known unique allelic allozymes that can be used to distinguish them (WARD & WARWICK, 1980; WARD & JANSON, 1985); however, the juveniles of the first species emerge from the brood pouches of their mothers, whereas the juveniles of the second emerge from benthic egg masses (HANNAFORD ELLIS, 1979). Recently MASTRO *et al.* (1982) used electrophoretic data to verify the status of the *L. scutulata* species complex, which has been previously separated into two species on the basis of penis shape and egg capsule morphology (MURRAY, 1979, 1982).

Another major contribution of allozyme electrophoresis to systematics is in the construction of phylogenies of closely related species (FERGUSON, 1980; BUTH, 1984). Electrophoretic data can be used to construct a phenetic or a phylogenetic classification using genetic distance data or using alleles as characters (WILEY, 1981; BUTH, 1984). A recent major advance in the construction of such phylogenies is the ability to put confidence limits on different

branches of the phylogeny by bootstrap methods (see FELSENSTEIN, 1985). This is necessary because usually several, and often many, cladograms with a similar degree of parsimony can be constructed from one character matrix (FELSENSTEIN, 1982, 1985).

In this paper we compare the morphology of *Littorina sitkana* Philippi, 1846, with that of *L. "kurila"* (REID, 1990) and with that of a wave-exposed shore taxon *Littorina* sp. All three taxa lay benthic egg masses which develop directly into juvenile snails (see BUCKLAND-NICKS *et al.* [1973] for *L. sitkana*; this paper for the other two taxa). These three taxa have very similar shell morphology and external anatomy and some gastropod systematists have lumped them together. Kohn examined the shell morphology and external anatomy of *L. sitkana* and *L. sp.* from Tatoosh Island, the major locality studied here, and concluded that both were the same species (A. J. Kohn, personal communication).

We used allozyme electrophoresis to distinguish *Littorina sitkana* and *L. sp.* on Tatoosh Island, Washington. The results of this enabled us to find more subtle morphological characters that make it possible to identify them in the field. We also had some success distinguishing the three taxa on the basis of shell shape alone; we used discriminant analysis of shell shape to classify adult *L. sp.*, *L. "kurila"*, and *L. sitkana* collected in the field and found that individual snails were assigned to the correct taxon 90% of the time. However, even multivariate analysis of shell shape can be misleading; when broods of *L. sp.* were split and cultured in the lab at two densities—but under otherwise identical conditions—the observed differences in shell shape were greater between the two densities than among field-collected snails of the three taxa. We also report the results of breeding experiments in which attempts were made to hybridize various populations of *L. sitkana*, *L. sp.*, and *L. "kurila"*. On the basis of reproductive characters, attempts at hybridization, and electrophoretic data from ten allozymes, we conclude that *L. sitkana* is distinct from *L. sp.* and also from *L. "kurila"*. Our allozyme evidence showed that *L. sp.* and *L. sitkana* were fixed for different alleles at three loci on Tatoosh Island, Washington. We show that *L. subrotundata* was closely related to *L. sp.* but was fixed for different alleles at the Pep-3 locus. *Littorina* sp. was closely related to *L. "kurila"* but was more distantly related to *L. sitkana*. We construct a preliminary phylogeny based on allozyme data for these and other taxa of *Littorina* from locations along the north-eastern Pacific and from Rhode Island in the northwestern Atlantic. We show that none of these North Atlantic species is conspecific with *L. sp.* or *L. sitkana*.

MATERIALS AND METHODS

Collection and Identification of Snails for Morphometry

Littorina sitkana was collected at ten sites from Siletz Bay, Oregon, north to Massacre Bay, Attu Island, Alaska

(Table 1). *Littorina* sp. was collected from six sites spanning from Whale Cove, Oregon north to near Sitka, Alaska (Table 1). More than 100 *L. "kurila"* were collected from Sweeper's Cove, Adak Island, Alaska (Table 1) at the same location and on the same field trip (VERMEIJ *et al.*, 1990) as some of the specimens used by D. G. Reid (REID, 1990); they were identical in size, shell coloration, and shape to specimen "m" in Reid's photograph labelled *L. kurila* (REID, 1990:4) and relabelled *L. "kurila"* in a note added in proof of REID (1990). We use *L. "kurila"* to refer to the Adak animals in what follows to avoid using *L. sp1* and *L. sp2*.

After collection, adult snails were held in free-flowing seawater in outdoor tanks at Friday Harbor Laboratories, Washington (Table 1). Openings were cut in 10 cm × 10 cm × 4 cm high polyethylene sandwich containers or 93-mm diameter petri dishes over which 1.1-mm nylon mesh was fastened with hot melt glue. This allowed water flow but did not permit the snails to escape.

Multivariate Analysis of Morphological Changes with Growth Rate

To see how shell morphology changed with growth rate, we used discriminant analysis to compare the morphology of cultured snails with that of snails collected in the field. The snails in our "field" collected treatments and the parents of snails in our experimental treatments were collected from the field: *Littorina* sp. was collected from the Finger on Tatoosh Island, *L. sitkana* was collected from North Island Draw on Tatoosh Island during 15–16 September 1989, and *L. "kurila"* was collected from Sweepers Cove on Adak (Table 1).

For our experimental treatments we cultured juveniles at various densities in dishes in outdoor tanks. The dishes were made by drilling 35-mm holes into the top and bottom halves of 93-mm diameter petri dishes. We used Optilux[™] petri dishes made by Falcon. These are made of clear styrene plastic, which lets most of the sunlight through and encourages algal growth inside the dishes. Nitex[™] mesh (243 μ m) was glued inside the holes in the top and bottom of the dish. A styrofoam float was glued to the outside of the top of the dish with hot melt glue. A pebble was placed inside each dish as ballast. The two halves of the petri dishes were held together by elastic bands. When the dish was placed in the water it filled and floated on edge, an orientation that allowed maximum water flow through the dish.

The dishes quickly became coated inside and outside with diatoms. The outside of each dish was cleaned periodically with a plastic scrub brush to allow in more light. This increased the biomass of diatoms growing on the inside of the dish where they were available to the snails. Dishes with a high density of snails were rasped clean on the inside of the dish; dishes with a lower density of snails had a visible coating of diatoms on the inside.

Table 1
Location of collection sites for electrophoresis.

Site		Species collected
Massacre Bay, Attu Is., Alaska	52°50'N, 173°40'E	<i>Littorina sitkana</i>
Sweeper Cove, Kuluk Bay, Adak Is., Alaska	51°51'N, 176°39'W	<i>Littorina sitkana</i> <i>Littorina "kurila"</i>
Hoonah, Alaska	58°08'N, 135°28'W	<i>Littorina sitkana</i>
Whitestone Harbor, Alaska	57°15'N, 135°34'W	<i>Littorina sitkana</i>
Bamfield, B.C.	48°50'N, 125°08'W	<i>Littorina</i> sp.
Tatoosh Is., Washington	48°23'N, 124°44'W	<i>Littorina sitkana</i> <i>Littorina</i> sp.
Shi Shi, Washington	48°16'N, 124°36'W	<i>Littorina</i> sp.
Waatch River, Mukkaw Bay, Washington	48°21'N, 124°40'W	<i>Littorina sitkana</i> <i>Littorina subrotundata</i>
Grays Harbor, Washington	46°54'N, 124°05'W	<i>Littorina subrotundata</i>
Siletz Bay, Oregon	44°56'N, 124°01'W	<i>Littorina sitkana</i>
Bass Rock Road, Rhode Island (South of Narragansett Pier)	41°25'N, 71°30'W	<i>Littorina littorea</i> <i>Littorina obtusata</i> <i>Littorina saxatilis</i>
Friday Harbor, Washington	48°30'N, 123°85'W	<i>Lacuna</i> sp.

We had two experimental treatments of *Littorina* sp. from Tatoosh: sparse and dense. The parents were collected from the field as juveniles (shell length 1.5–2.5 mm) and were isolated in unsexed pairs in culture dishes with 243- μ m Nitex[®] mesh over the openings. The sex ratio of the parents was not significantly different from 50:50 and 22 out of 23 of the pairs with one female and one male produced egg masses which hatched between October 1987 and June 1988. The eggs remained in the parents' dishes until the largest juvenile in a dish had reached a shell length of about 1 mm. The juveniles were then split into two initial densities: sparse (10 juveniles per dish) and dense (30 juveniles per dish). To split the broods, the largest 40 juveniles were first divided into two groups of 20 by starting with the largest juvenile and placing it in the first group, then putting the second largest in the second group, then the third largest in the first group, and so on. Then the first group was split into two groups of 10 using the same procedure. The dense dish contained the other group of 10 plus the group of 20. A random number table was used to decide whether the largest juvenile was put in the first or second group but the rest of the procedure was done systematically. Some mortality occurred soon after this procedure so that the density of the sparse treatments at the time of measuring ranged from 2 to 9 with a mean of 6 (SD 2.3, $n = 15$); the density of the dense treatments ranged from 6 to 15 with a mean of 12.7 (SD 3.3, $n = 15$). These are referred to as the "sparse *L. sp.*" treatment and the "dense *L. sp.*" treatment respectively. Other *L. sp.* were raised loose in a large plexiglass tank about 1 m \times 2 m \times 0.5 m deep.

We had one experimental treatment of *Littorina* "*kurila*," the dish *L. "kurila"* treatment. *Littorina* "*kurila*" from Adak Island were raised by removing eggs close

to hatching from the sandwich containers of their parents and placing them in a culture dish. The early juvenile stages were reared at densities from 18 to 27 per dish with a mean of 23.7, while later juvenile stages were raised at densities of 1 to 14 with a mean of 7.6 (SD 4.35, $n = 18$). At the time of measuring, the densities ranged from 1 to 14 with a mean of 6.35 (SD 4.0, $n = 30$).

We had one experimental treatment of *Littorina sitkana*, the "tank *L. sitkana*" treatment. *Littorina sitkana* from Tatoosh Island were raised in culture dishes at densities from 1 to 10 adults per dish and also loose in a large tank about 1 m \times 2 m \times 0.5 m deep. The diatom growth in this large tank was never significantly reduced by the grazing of snails and the maximal growth rates of *L. sitkana* exceeded those measured in the field (BOULDING, 1990b; Boulding & Van Alstyne, unpublished data).

Snails from other locations (Table 1) were also held in petri dishes and some of these produced young; the shell morphology and external anatomy of these snails was also examined by E. G. Boulding but no multivariate analysis was done.

Shell Measurement

Shells were videotaped under a dissecting microscope then digitized with an image analysis system. Preliminary work (BOULDING & HAY, in press) showed that most of the measurement error using this technique came from variation in the way the shell was oriented. Therefore the shell was consistently photographed in two orientations. In the "axial orientation" (Figure 2a) the shell was oriented so that a line joining the apex and base of the columella was in the plane perpendicular to the optical path and so that the curve of the last (body) whorl was just

hidden by the outer lip of the aperture. In the "apertural orientation" (Figure 2b) the shell was oriented so that the outer rim of the aperture was in the plane perpendicular to the optical path. To reduce errors resulting from inconsistent orientation, an acetate grid was taped over the video monitor and used to ensure that the axis of coiling was always parallel with the horizontal grid lines of the monitor.

Each snail's video-frame number, dish number, grade of spiral sculpture, shell color classification, and wet weight were entered in a database at the time of videotaping. Shell sculpture was graded as 0 to 3, 0 being completely smooth and 3 being deeply ridged. The grades were not equivalent for *Littorina sitkana* and *L. sp.* since the most developed spiral sculpture ever seen for *L. sp.* did not reach that of *L. sitkana*. For this reason spiral sculpture was not included in the discriminant analysis.

The measurements shown in Figure 2 (standard error for repeated measurements of shell length was 0.01 mm; BOULDING & HAY, in press) were chosen because they could be taken nondestructively on a living snail with a high degree of repeatability and because they are comparable to those taken with calipers on larger snails by previous investigators. We measured diameters instead of radii as recommended by Schindel (unpublished manuscript). A Pascal program was written to locate the axis of coiling and to calculate the desired measurements from the digitized points. The axis of coiling was estimated by bisecting the angle formed by the three points marked with dots in Figure 2a. Shell length (SL) was defined as the maximum distance between the apex and a line tangential to the base of the columella and perpendicular to the axis of coiling. Shell width (SW) was measured perpendicular to shell length and was defined as the distance between the line tangent to the points on the left and right outlines of the body whorl farthest from the axis of coiling (Figure 2a). The whorl width at suture (WW) was defined as the distance between the upper and lowermost points marked on the suture above the last (body) whorl (Figure 2a). The outer margin of the aperture was digitized to measure aperture area (AA) (Figure 2b). The aperture length (AL) was the maximum distance between point of adhesion (PA; Schindel, unpublished manuscript) in apertural view (Figure 2b) and a point on the other side of the outer aperture. Aperture width (AW) was the maximum width of the outer aperture perpendicular to aperture length.

Multivariate Analysis of Shell Shape

We used program 7M of the BMDP Statistical Software Package (JENNRICH & SAMPSON, 1985) to do stepwise discriminant analysis and canonical variate analysis on the variables SL, SW, WW, AL, AW, and AA. We identified the snails to taxon using the characters described in the comparative morphology section of the results; this can be done with 100% accuracy for animals larger than 2 mm and our ability to do this correctly for the sympatric species pair, *Littorina sitkana* and *L. sp.*, has been confirmed by

allozyme electrophoresis. There were seven treatments: tank *L. sitkana*, field *L. sitkana*, dish *L. "kurila,"* field *L. "kurila,"* sparse *L. sp.*, dense *L. sp.*, and field *L. sp.* as described above, and each treatment was assigned a grouping variable. All variables were log-transformed before the analysis to stabilize variance and the "jackknife" option was used. This ensured that the classification function used to determine group assignment was unbiased since the snail being classified had not been used to construct the function. We ran the program 7M twice: the first time we used only the three field treatments and the second time we used all seven treatments.

Other Measurements

We assessed size at sexual maturity for females by measuring the shell length at which a female confined with a mature male began to lay eggs; the size at sexual maturity for males was the size at which the penial glands of a male were fully developed. We determined wet weight to the nearest 0.1 mg by blotting a live snail and placing it on the tray of a Sartorius balance (model 2404). We determined foot area for *Littorina sitkana* and *L. sp.* from Ta-toosh by photographing the foot of a snail actively crawling over an inverted petri dish. We used analysis of covariance (ANCOVA) with the program BMDP 1V, using an estimate of shell volume ($SL \times SW \times SW$)^{0.66} as the covariate to test whether the mean foot area was greater for *L. sp.* than for *L. sitkana*. We also used ANCOVA with shell volume as the covariate to test whether mean wet weight was greater for *L. sitkana* than for *L. sp.*

Hybridization Experiment

Pairs of juvenile littorinids measuring 1.5–2.5 mm in shell length were selected at random from a large group and put in culture dishes. The dishes were inspected at intervals between 14 April and September 1988 for the presence of eggs. The snails were not sexed before putting them in the dishes so only about half the dishes contained one male and one female snail. During the study some snails died and were replaced with another small juvenile snail measuring 1.5–2.5 mm. Only a few of these unsexed crosses involved *Littorina sitkana* as this first hybridization experiment was done for another purpose (BOULDING & HAY, in press).

A second hybridization experiment was done to see whether different populations of *Littorina sitkana* were capable of crossing with each other (Table 6). This second experiment also included some crosses between *L. sp.* and *L. sitkana*. In each dish one virgin female snail (defined as a female isolated from males since before it reached 2.5 mm in shell length) and one male snail were put together. The dishes were put in an outdoor tank with free-flowing seawater in August 1988. An attempt was made to put an intrapopulation pair together for every interpopulation pair (Table 6). We tried to cross males and females from each site with those from other sites but for some sites no virgin

Table 2
Enzymes screened for all species.

Enzyme	Enzyme	Synonym	E.C. No.	n ¹	Locus	Buffer	Migration ²
aspartate aminotransferase	Aat	Got	2.6.1.1	2	Aat-1	I	0.74
esterase	Est	Est α NA	3.1.1.1	?	Est-2	I	1.15
β -N-Acetylgalatosaminidase	β -Gala	β -Gal	3.2.1.53	1	β -Gala-1	III	0.74
N-Acetyl- β -glucosaminidase	β -Ga	β -Glu	3.2.1.30	1	β -Ga-1	III	0.67
glucose-6-phosphate isomerase	Gpi	Pgi	5.3.1.9	2	Gpi-1	I	0.95
peptidase	Pep		3.4.11	3	Pep-2	I	0.98
					Pep-3	I	0.58
phosphoglucomutase	Pgm		2.7.5.1	3	Pgm-1	II	1.52
6-phosphogluconate dehydrogenase	6-Pgd	Pgdh	1.1.1.44	1	6-Pgd	III	0.59
sorbitol dehydrogenase	Sdh	Iddh	1.1.1.14	4	Sdh-4	II	0.33
					Sdh-1 ³	II	0.98

¹ Number of loci observed.

² Migration of 100 allele relative to slow red dye (magenta) of red food coloring.

³ Not available for *Lacuna*.

females were available. The dishes were inspected periodically for the presence of eggs until August 1989 and the number of dishes that produced fertile eggs was recorded. We occasionally obtained infertile eggs in watery jelly that did not develop, but we did not count these because we also obtained these from virgin female-virgin female pairs of the same species that were left together for a long period.

Collection and Identification of Specimens for Electrophoresis

Littorina sitkana were collected from seven sites, *L. sp.* from three sites, *L. subrotundata* from two sites, and *L. scutulata* from one site along the northeastern Pacific coast. For comparison, *L. saxatilis*, *L. littorea*, and *L. obtusata* were collected from Rhode Island in the northwestern Atlantic (Table 1). *Littorina "kurila"* was collected from Sweeper's Cove, Adak Island, Alaska (Table 1) at the same location and on the same field trip as the Adak Island specimens discussed by REID (1990).

Littorina sitkana, *L. "kurila"*, and *L. sp.* were identified using the morphological criteria described below in the Results section. The *L. scutulata* were identified as true *L. scutulata* Gould, 1849, because the females had egg capsules with unequal rims (MASTRO *et al.*, 1982). The *Lacuna* were identified as *Lacuna vineta* (Montagu, 1803) using KOZLOFF (1987).

David G. Reid identified the *Littorina saxatilis* as true *L. saxatilis* Olivi, 1792 (= *L. rudis* Maton 1797; FRETTER, 1980). The *L. saxatilis* shells were large (shell height 9.0–11.0 mm), heavy, and ridged, and the females were ovoviviparous. He identified the *L. obtusata* shells as true *L. obtusata* on the basis of their shape and relatively large size (shell length 8.0–10.0 mm).

The *Littorina subrotundata* (= *Algamorda subrotundata* Carpenter, 1864) (= *Littorina newcomiana* Hemphill, 1876

[REID, 1989]) were collected and identified by D. G. Reid. Note that we are using this name in its strict sense to refer only to the salt marsh form mentioned by REID & GOLIKOV (1991).

Enzyme Assay Technique

Snails were held in running seawater for at least a week and allowed to graze on benthic diatoms. Some individuals were stored at -80°C until they were used and others were used alive. The entire body of each snail was used except for the embryos brooded by female *Littorina saxatilis*. The body was homogenized in an equal weight of 0.5 M Tris-HCl buffer of pH 7.1. The crude homogenate was absorbed onto 12×2.5 mm wicks of Whatman No. 1 filter paper and 24–30 wicks were placed into a horizontal gel of 12.5% Sigma starch. Narrower wicks were dipped into red food coloring (FD&C Red No. 3 and Red No. 40) and placed between every six sample wicks. The buffer systems used were: (I) discontinuous, tris-citrate electrode buffer, pH 8.65, borate (NaOH) gel buffer, pH 8.1 (AYALA *et al.*, 1973); (II) continuous, tris-borate-EDTA electrode and gel buffer, pH 9.1 (AYALA *et al.*, 1973); and (III) amine, citric acid buffer, pH 7.0 (CLAYTON & TRETIK, 1972). The buffer used for each enzyme and synonyms for enzyme names are shown in Table 2.

Enzyme staining procedures followed those of MASTRO *et al.* (1982) for Aat, Est α NA, Gpi, Lap, Mdh, Pgm, and Sdh, and those of AEBERSOLD *et al.* (1987) for Est-D, β -Gala, β -Ga, 6-Pdg (with double the amount of NADP), Pep-2 (substrate glycyl-L-leucine), Pep-3 (substrate L-leucyl-L-tyrosine and L-leucyl-L-valine), Pgm-agar (with double the amount of NADP and G6PDH). Sod was read off the Sdh gels. Sod, Est α NA, Lap, and Mdh were not assayed for all species.

When more than one locus was resolved for an enzyme, the fastest migrating locus is given the suffix 1, the next fastest 2, and so on. For each locus the most common allele

in the Tatoosh Island population of *Littorina sitkana* is labelled as 100. The average distance of migration of the slow red dye (magneta) was 40 mm and of the fast red dye (orange-red) was 120 mm. The absolute distance of migration of the 100 allele of each locus relative to that of the slow red dye is given in Table 2. An allele which was 5 mm slower than the 100 allele on an average gel would be labelled 95 whereas one that was 12 mm faster would be labelled 112.

Although more than one locus was resolved for most enzymes (Table 2), usually only one locus could be scored. The products of fainter loci for the same enzyme were often obscured by an allele of a darker locus for at least one species out of the nine.

Three loci were resolved for the peptidases (Table 2). The substrate glycyl-L-leucine gave a faint fast band, a dark medium band, and a faint slow band, and the substrate L-leucyl-L-tyrosine with L-leucyl-L-leucine gave a faint fast band and dark medium and slow bands.

The Est α NA stain gave at least five regions of activity (Figure 8a). Although esterases have been used in many studies of *Littorina* (see BERGER, 1973; JANSON & WARD, 1984), no studies on *Littorina* have been published showing a Mendelian pattern of inheritance for any of the zones scored as corresponding to loci. On our gels there are at least five regions of activity which we will equate to loci for the purpose of discussion (Figure 8a). We did not use the esterase data in our phylogenetic analysis; we present the qualitative results only.

The Pgm-1 locus is a compound locus probably representing a recent duplication. The locus was scored as if the snails were tetraploid with the alleles of the same mobilities present at both loci, something that is commonly seen in plants (R. Laushman, personal communication). For example in Figure 8b the snails in lanes 5–8 have two copies of the allele *Pgm-1*⁹⁸, one copy of *Pgm-1*¹⁰² and one copy of *Pgm-1*¹⁰⁴; the snails in lanes 9–10 have four copies of *Pgm-1*⁹⁸; and the snail in lane 11 has two copies of *Pgm-1*¹⁰² and two copies of *Pgm-1*¹⁰⁴; and the snail in lane 12 has two copies of *Pgm-1*⁹⁸ and two copies of *Pgm-1*¹⁰². All are *Littorina subrotundata* from Gray's Harbor, Washington.

Data Analysis

The allele frequency data were analyzed first using Biosys-1, release 1.7 (SWOFFORD & SELANDER, 1989). We calculated Nei's (1972, 1978) unbiased genetic distance. We constructed a distance-Wagner tree based on 10 loci from 13 operational taxonomic units (= OTUs; FARRIS, 1981) using SWOFFORD's (1981) multiple addition criterion on CAVALLI-SFORZA & EDWARDS' (1967) chord distance. *Littorina littorea* was used as the outgroup instead of *Lacuna*, as was done in BOULDING (1990b), because *L. littorea* shared the fewest alleles with the other littorinid species and because the cladistic analysis of morphology for the genus *Littorina* showed *L. littorea* was morpholog-

ically distant from the other littorinid species considered here (REID, 1990).

Bootstrapping was used to obtain confidence limits on the validity of different groupings of the OTUs suggested in the phylogenies (FELSENSTEIN, 1985). To do this a bootstrapping program was written in Turbo Pascal 5.0 to generate different input files for Biosys-1. Each input file contained 10 enzyme loci for all 13 OTUs. The 10 enzyme loci in the input file were chosen randomly with replacement from the 10 original loci for each analysis. Thus, in each input file some of the original 10 loci might be absent and others might be duplicated. For example the first bootstrap run of Biosys-1 might have used Aat-1, Aat-1, Sdh-4, Pgm-1, Pgm-1, 6-Pdg, 6-Pdg, 6-Pdg, Pep-3, and Gpi, whereas the second run might have used Pep-2, Pep-3, Pep-3, Pep-3, Sdh-4, Sdh-4, Pgm-1, Gpi, Gpi, and 6-Pdg, and this was continued until 100 runs had been made. The output from these 100 runs was then examined and a tally was made of the number of times certain groups of OTUs appeared together. For the distance-Wagner analysis, the cluster was considered discrete if the distance between the two groups was at least twice that of the distance between any two OTUs in the group. When a group of OTUs appeared clustered together at least 95 times out of 100 during the bootstrapping, this was taken as significant support for that grouping in the original phylogeny. Some OTUs changed branching orders and distances between nodes on more than 5% of the bootstrap replicates; this meant that portion of the tree was not fully resolved by our data.

RESULTS

Field Characters of *Littorina* from the Northeastern Pacific

Our culture experiments and allozyme data allowed us to identify several characters that in combination allow separation of these taxa in the field. The shell of *Littorina* sp. either lacked spiral sculpture (Figure 1a, g–i), or had a few spiral grooves (Figure 1d), or occasionally had spiral sculpture consisting of shallow, evenly spaced, undulating, spiral ridges more than twice the width of the grooves between them. The shell of *L. sitkana* could be smooth (Figure 1e) but usually had deep spiral ridges that were unevenly spaced and were less than twice as wide as the intervening grooves, and often had small riblets in the grooves and on the large ridges (Figure 1b). The shell of *L. sitkana* (Figure 1b, e) typically was lower spired (shell width 0.86 of shell length) than that of *L. sp.* The shell of *L. "kurila"* (Figure 1c, f) from Adak Island was typically larger than that of *L. sp.* and had a higher spire. The operculum of *L. sp.* appeared light tan on a live animal whereas the opercula of *L. sitkana* and of *L. "kurila"* appeared dark.

Color differences were also noticeable on the body. *Littorina* sp. had cephalic tentacles that were yellow or light gray with a dark gray line along the edge above the eye

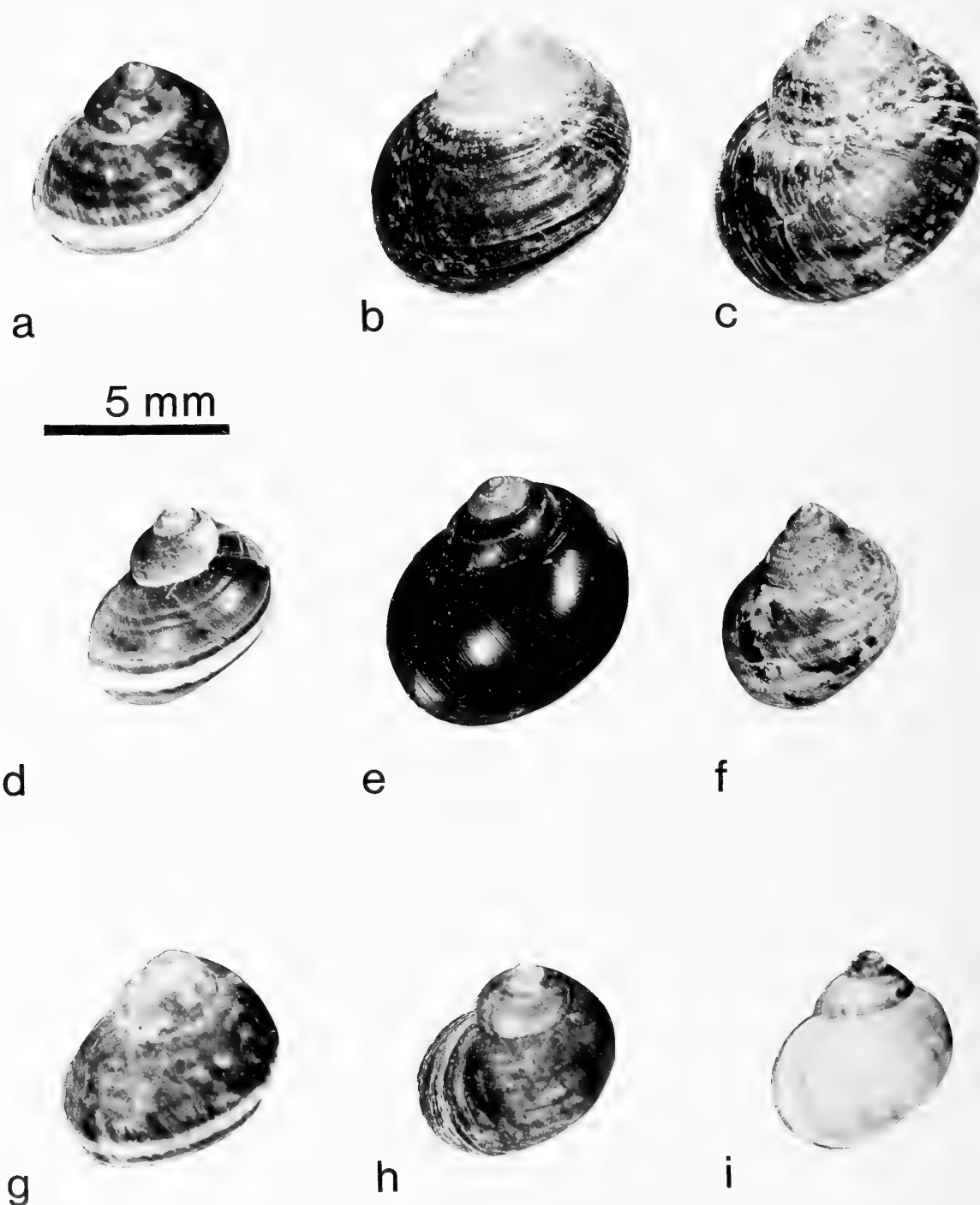


Figure 1

Specimens of *Littorina* sp. (a, g, h, i), *L. sitkana* (b), and *L. "kurila"* (c) collected in the field. Specimens of *L.* sp. (d), *L. sitkana* (e), and *L. "kurila"* (f) cultured at Friday Harbor for one generation from parents collected in the field. Specimen (a) is *L.* sp. SL = 5.6, SB = 5.3, SW = 5.0, AH = 3.9, AW = 3.2 USNM 860183; specimens (g, h, i) are three additional specimens of *L.* sp. USNM 860184: (g) SL = 6.6, SW = 6.0, (h) SL = 5.9, SW = 5.5, (i) SL = 5.0, SW = 4.3. SL is greatest shell length with one jaw of caliper on apex, SB is greatest shell breadth from outer lip of aperture, SW is shell width taken perpendicular to length, AH is greatest aperture length, and AW is aperture width perpendicular to aperture length; all measurements were taken with digital calipers in millimetres. The smooth *L. sitkana* (e) was cultured to adult size at a high growth rate in our "tank treatment" from parents that had deep spiral ridging as shown by specimen (b).

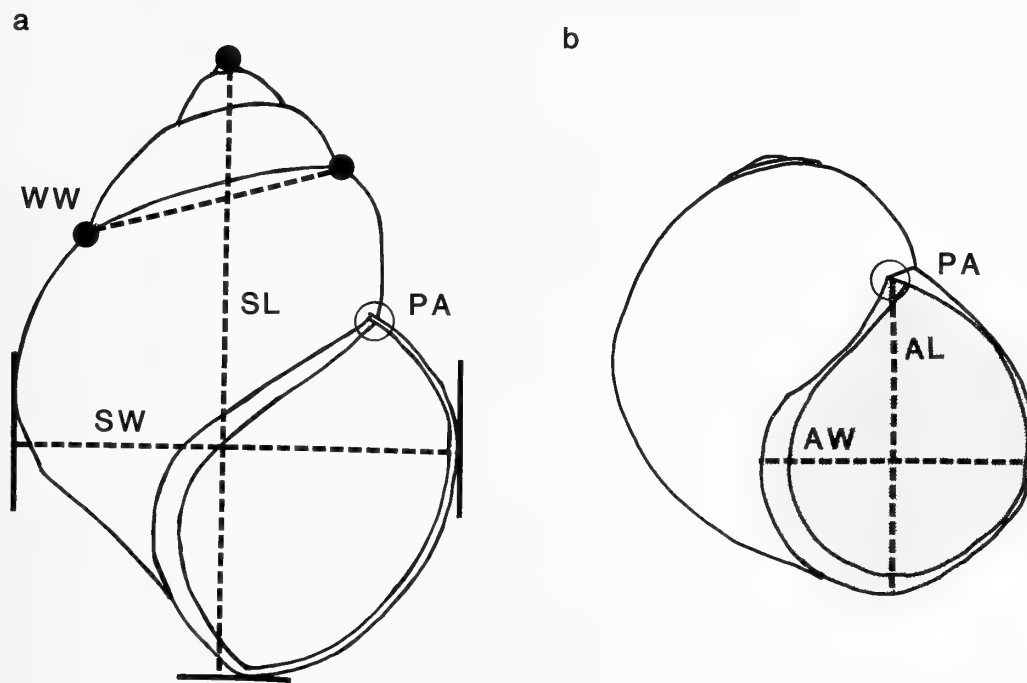


Figure 2

Measurements made on shells digitized with video digitizing system. a. Measurements taken on axial view. b. Measurements taken on apertural view. SL = shell length; SW = shell width; WW = distance between sutures of whorl above body whorl; PA (circled) = point of adhesion (of aperture to body whorl); AL = aperture length; AW = aperture width; shaded area = AA, area of outer aperture. Dots indicate points used for calculating apical angle; see text.

and dark gray pigment on the head. The pigmentation of its tentacles was slightly darker in larger animals. The sides of its foot were yellow, and the sole was pale. In contrast *L. "kurila"* had black cephalic tentacles and the sides of its foot were black; male *L. "kurila"* had black pigmentation on the dorsal side of the penis. The body of *L. sitkana* was also dark with black cephalic tentacles and black pigmentation on the dorsal side of the penis. Some tall-spined *L. sp.* resembled *L. scutulata* but the outer lip of the aperture of *L. scutulata* joined the body whorl at an angle of less than 45 degrees (*cf.* Figure 2a) and the penis of male *L. scutulata* had a distinct hooklike filament near the end (MURRAY, 1979).

The egg masses of *Littorina sitkana* were larger and had a less viscous jelly than did those of *L. sp.* There were also differences in mean adult body size. Whereas it was rare to find a *L. sp.* larger than 5 mm in the field, *L. sitkana* had a mean adult size of 9 mm or larger (Boulding & Van Alstyne, in review). The *L. "kurila"* collected at Adak were mostly over 9 mm in height.

Shell color and pattern was also useful in distinguishing these taxa. Common color morphs of *Littorina sp.* included dark brown to olive throughout (Figure 1h); gray to white throughout (Figure 1i); dark brown to olive to orange background with a narrow white to orange band(s) just abapical of the widest part of the last (body) whorl (Figure 1g); brown to olive to light gray background with dark

brown stripes, often with a narrow white to orange band just abapical of the widest part of the last whorl (Figure 1a, d); and purple to pinkish background with white stripes. The shell of *L. sitkana* was usually dark black-brown to dark olive throughout but a common variant had alternate white and black bands. Completely white *L. sitkana* were sometimes found. The shell of *L. "kurila"* on Adak Island was usually dark brown or gray and often had dark brown spiral stripes.

Multivariate Analysis of Shell Shape

The most interesting result from this analysis was that the amount of within-taxon variation in shell shape could exceed that typically observed between taxa. The ratios of whorl width at suture to shell length, and of square root of aperture area to shell length were similar among shells of field *Littorina sitkana*, tank *L. sitkana*, dish *L. "kurila"*, field *L. "kurila"*, dense *L. sp.*, and field *L. sp.* (Table 3). However, the shells of *L. sp.* from the sparse treatment were appreciably narrower with narrower apertures and consequently smaller apertural areas (Table 3). They also weighed significantly less (ANCOVA, $P < 0.05$, covariate $SL \times SW \times SW$) than their siblings in the dense treatment. The field *L. sitkana* weighed significantly more than the other six treatments (ANCOVA, $P < 0.06$, covariate $SL \times SW \times SW$).

Table 3
Means, standard deviations, and mean ratio to shell length of morphometric variables used in multivariate analyses of *Littorina* species.

	<i>L. sitkana</i>		<i>L. "kurila"</i>		<i>L. sp.</i>		
	Tanks	Field	Dishes	Field	Sparse	Dense	Field
<i>n</i>	25	39	30	36	37	47	33
Means							
SL	6.56	8.97	5.89	9.55	6.43	4.57	5.75
SW	5.77	7.74	5.14	7.29	4.41	3.85	4.77
WW	2.23	2.99	1.98	3.21	1.89	1.59	4.87
AL	4.81	6.49	4.11	6.45	4.18	3.01	3.86
AW	3.89	5.30	3.55	5.12	3.04	2.58	3.28
AA ^{0.5}	13.31	25.03	10.65	22.42	7.84	5.68	9.32
Standard deviations							
SL	1.48	1.62	1.38	0.85	0.83	0.52	1.39
SW	1.17	1.19	1.14	0.68	0.56	0.45	0.76
WW	0.51	0.58	0.42	0.26	0.29	0.18	0.35
AL	0.95	1.08	0.96	0.71	0.53	0.37	0.65
AW	0.84	0.88	0.90	0.58	0.43	0.30	0.55
AA ^{0.5}	5.76	7.93	5.49	5.26	2.05	1.35	3.72
Ratios							
SL	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SW	0.88	0.86	0.87	0.76	0.68	0.84	0.83
WW	0.34	0.33	0.34	0.34	0.30	0.35	0.33
AL	0.73	0.72	0.70	0.64	0.65	0.66	0.67
AW	0.59	0.59	0.60	0.54	0.47	0.56	0.57
AA ^{0.5}	0.56	0.56	0.55	0.50	0.44	0.52	0.53

The first stepwise discriminant analysis of only the three field treatments selected a classification function consisting of the variables shell length (SL), shell width (SW), aperture length (AL), and aperture area (AA; Table 4). The jackknifed classification function correctly classified 92% of the *Littorina sitkana*, 89% of the *L. "kurila"*, and 91% of the *L. sp.* into the correct group (Table 4). The plot of the first and second canonical variables shows almost complete separation of the field *L. sitkana* (I) from the field *L. sp.* (A) and partial separation of the field *L. "kurila"* (U) from the other two groups (Figure 6).

A subsequent analysis including all seven groups yielded a discriminant function containing the variables shell length, shell width, and aperture length (Table 5). This classification function varied in its ability to correctly classify specimens from a high of 94% for the sparse *Littorina sp.* to a low of 37% for the dish *L. "kurila"* (Table 5). The misclassifications were not necessarily into another treatment of the same taxa (BOULDING, 1990b). The plot of the first two canonical variables separated out the sparse *L. sp.* (T) and partially separated field *L. sitkana* (I) from the other six groups along the axis of CV1. The dense *L. sp.* (D) was separated from the field *L. "kurila"* (U) along the axis of CV2 (Figure 7).

As is typical in discriminant analyses, the composition of the canonical variables was very different for the three group and the seven group analyses. The standardized coefficients for CV1 for the canonical variate analysis for

the three field taxa were large and positive for shell width and aperture length, and large and negative for shell length and aperture area (Table 4). The standardized coefficients for CV1 from the canonical variate analysis for all seven treatments were large and positive for shell width and large and negative for shell length (Table 5). The standardized coefficients for CV2 for the three taxa analysis were large and positive for shell length and smaller and positive for shell width (Table 4). The standardized coefficients for CV2 for the seven treatments were large and negative for shell width and smaller and positive for shell length and aperture length (Table 5). In no case was the rank order of the groups along the axis of a canonical variable correlated with their mean size (as determined by shell length).

Shell Sculpture

The *Littorina sitkana* grown at high growth rates in the tank treatment were either completely smooth or had only one to a few ridges abapical to the widest part of the last whorl. This occurred even though these snails all had parents with deep spiral ridging. Some smooth *L. sitkana* were also collected from the field at Tatoosh Island and at other locations.

Littorina sitkana cultured in dishes at low densities were also often smooth even though their field-collected parents had had deep spiral ridging. Eleven out of 21 *L. sitkana* juveniles from Tatoosh that were isolated in pairs and then

Table 4

Discriminant analysis of field collected snails of three *Littorina* taxa: *L. sitkana*, *L. "kurila"*, and *L. sp.*

Classification function			
Group	<i>L. sitkana</i>	<i>L. "kurila"</i>	<i>L. sp.</i>
% correctly classified	92%	89%	91%
Variable			
ln(SL)	26.72	92.99	73.92
ln(SW)	416.10	357.72	347.25
ln(AL)	419.94	384.37	344.80
ln(AA ^{0.5})	-365.30	-355.45	-332.46
Constant	-266.08	-258.93	-202.71
Standardized coefficients for canonical variables			
	Can. var. 1	Can. var. 2	
Variable			
ln(SL)	-1.61	-3.13	
ln(SW)	2.11	1.79	
ln(AL)	2.56	0.30	
ln(AA ^{0.5})	-2.30	0.47	
Constant	-14.99	8.67	

cultured in dishes were completely smooth and the rest had weak sculpture. Twenty-three pairs of juveniles from San Juan Island that were isolated in dishes grew up to be smooth even though their field-collected parents had been strongly ridged. Ten *L. sitkana* whose parents had been deeply ridged when collected from Hoonah, Alaska, grew up to be completely smooth when grown in pairs in

culture dishes. Juvenile *L. sitkana* grown more slowly at higher densities were more likely to be ridged.

Littorina sp. were grown at a range of densities at different times of the year. Some *L. sp.* developed fine ridges when grown slowly but no *L. sp.* ever attained the deep spiral ridging that is typical of *L. sitkana* collected in the field. When present the ridges of cultured *L. sp.* were evenly spaced and more than twice the width of the grooves between them, whereas the ridges of cultured *L. sitkana* were unevenly spaced and less than twice as wide as the intervening grooves.

Aperture

Littorina sp. from the sparse treatment had a narrower aperture for its size than *L. sp.* from the dense treatment, the latter being similar in width to *L. sitkana* (Table 3; ANCOVA with shell length as covariate, $P < 0.05$). The inner lip of the *L. sitkana* aperture is more flared towards the base of the columella than is that of *L. sp.*, such that there is a greater difference between the outer area (as measured; Figure 2b) and the inner area (which the operculum closes).

Size

Littorina sitkana reached sexual maturity at a larger size (shell length: females 5.5–7.0 mm, males 4.2–6.0 mm) than *L. sp.* (females 3.8–5.5 mm, mean = 5.25 [SD 0.47]; males 3.3–5.0 mm, mean = 4.85 [SD 0.52] $n = 137$). Preliminary data suggested that when raised at Friday Harbor, *L. "kurila"* became mature at a greater shell length than the other two taxa (females about 6.0 mm, males about 4.8 mm).

Table 5

Discriminant analysis of all seven groups of snails (*Littorina*).

Classification function							
Group	<i>L. sitkana</i>		<i>L. "kurila"</i>		<i>L. sp.</i>		
	Tanks	Field	Dishes	Field	Sparse	Dense	Field
% correctly classified	56%	82%	37%	86%	94%	83%	51%
Variable							
ln(SL)	79.5	82.1	96.7	146.4	178.5	124.7	119.9
ln(SW)	105.0	113.7	113.1	74.5	-17.4	94.4	90.6
ln(AL)	-114.1	-112.3	-77.3	-112.2	-80.2	-67.4	-76.3
Constant	-78.5	-102.3	-77.3	-112.2	-80.2	-67.5	-76.3
Standardized coefficients for canonical variables							
	Can. var. 1	Can. var. 2	Can. var. 3				
Variable							
ln(SL)	-2.55	1.18	-2.40				
ln(SW)	3.00	-2.04	-1.35				
ln(AL)	0.07	1.67	3.45				
Constant	-4.43	-6.85	9.64				

Animal

Males of all three taxa had a thick penis with a dorsal sperm groove, and a row of mammilliform glands along the convex edge nearly to the tip. The penis of *Littorina* sp. was yellow with 7–11 mammilliform glandular papillae in a single row, a dorsal sperm groove, and a short tip (Figure 3c). In general the number of penial glands increased with body size within any taxon. Sexually mature *L. sitkana* males had between 7 and 18 glands with a mean of 13 (shell lengths 6.0–10.0 mm, $n = 13$). The largest *L. sitkana* found (shell length 25 mm) had 22 penial glands arranged in two rows. *Littorina* sp. males had between 7 and 11 glands with a mean of 9 (shell lengths 3.5–5.0 mm, $n = 11$). *Littorina* “*kurila*” males had between 15 and 17 glands (shell lengths 4.8–6.4 mm, $n = 3$). Foot area measured by photographing the snail while it was crawling on an inverted petri dish was significantly greater for *L. sp.* than for *L. sitkana* (ANCOVA, $P < 0.007$, covariate = [SL \times SW \times SW]^{0.66}).

Reproduction

These snails all have an egg capsule surrounding a single egg (Figure 4a–c). The egg capsule of *Littorina sitkana* has a thick-walled side and a thin-walled side (BUCKLAND-NICKS & CHIA, 1990; Figure 4a, d) but the capsules of *L. sp.* and *L. “kurila”* have walls of equal thickness all the way around (Figure 4b, c, e). *Littorina sitkana* frequently lays communal egg masses which can reach 100 mm in diameter whereas *L. sp.* never does. Indeed a large *L. sp.* will frequently lay several small egg masses in quick succession. The egg masses of *L. “kurila”* are similar in size to those of *L. sp.* The time to hatching and the color changes of developing *L. sitkana* are very similar to those of *L. sp.*, and both species have only one egg per egg capsule (BUCKLAND-NICKS *et al.*, 1973; Boulding, unpublished data).

Radula

All these snails have very similar radulae (Figure 5). The outer marginal teeth in *Littorina sitkana* had 7 or 8 cusps ($n = 5$) (see also ROSEWATER, 1979), those of *L. “kurila”* had 6 or 7 cusps ($n = 2$) and those of *L. sp.* 9 or 10 cusps ($n = 5$). The lower edge of the base of the rachidian is not as deeply scalloped for *L. sitkana* as for *L. sp.* (Figure 5a, b).

Geographic Ranges

The confirmed geographic range of *Littorina* sp. is from Sealion Rocks, Sitka, Alaska (57°03'N, 135°20'W) to at least as far south as Cape Argo, near Coos Bay, Oregon (43°N, 124°W), based on live specimens examined by E. G. Boulding. We suspect *L. sp.* extends as far north as St. Lawrence Island (62°50'N, 169°50'W), based on shells examined by E.G.B. at the U.S. National Museum (USNM) during July 1990.

In contrast, *Littorina sitkana* has a range from northern Japan to the Aleutian Islands (REID & GOLIKOV, 1991) south to Charleston, Oregon (BEHRENS YAMADA, 1977a, b). *Littorina* “*kurila*” has a range from St. Paul's Island (57°00'N, 171°00'W) and from Akutan Pass (54°00'N, 166°00'W) through the Aleutian Islands (based on specimens examined by E.G.B. at the USNM) to the southern Kurile Islands (as *L. subrotundata* in REID & GOLIKOV, 1991). Thus the ranges of *L. sp.* and *L. “kurila”* may overlap in the Aleutian Islands, but this is difficult to confirm when only shells are available.

Hybridization Experiments

In the first experiment, none of the 95 dishes with one unsexed *Littorina sitkana* and one unsexed *L. sp.* produced fertile eggs, while 44% of the unsexed *L. sp.* \times *L. sp.* did so (BOULDING, 1990b). Some of the unsexed *L. sitkana* \times *L. sp.* crosses laid infertile eggs that failed to develop but infertile eggs were also laid by isolated, virgin, adult females.

In the second experiment, fertile eggs were produced when northern *Littorina sitkana* from the Aleutians were crossed with southern *L. sitkana* from Oregon (Table 6). All other crosses done between different populations of *L. sitkana* also gave rise to fertile eggs (Table 6). None of the four dishes with a female *L. sp.* from Tatoosh and a male *L. “kurila”* from Adak produced eggs (Table 6).

Allozyme Electrophoresis

Allozyme variability: On Tatoosh Island *Littorina scutulata* ($h = 0.177$) had a higher mean heterozygosity per locus than *L. sitkana* ($h = 0.007$) or *L. sp.* ($h = 0.070$). The mean sample sizes per locus were 29.5, 36.9, and 40.8 respectively.

Diagnostic loci for differentiating *Littorina sitkana* and *L. sp.*: On Tatoosh Island (Table 1) there are fixed or nearly fixed differences at four loci between *L. sitkana* and *L. sp.* (Table 7). At the Gpi-1 locus, *L. sp.* is nearly fixed for a slower allele than *L. sitkana*, at the Sdh-4 locus *L. sp.* is nearly fixed for a faster allele than *L. sitkana*, at the Pep-3 locus *L. sp.* is fixed for a slower allele than *L. sitkana*, and at the Pgm-1 locus *L. sp.* does not share alleles with *L. sitkana* (Figure 8b, Table 7). Indeed Sdh-4 is probably a tetramer and heterozygotes appear as streaks in *L. scutulata*, which clearly has several alleles. In *L. sitkana* we saw only a few streaks for Sdh-4 and no homozygotes for the *Sdh-4*¹⁰⁸ allele fixed in *L. sp.* (Table 7); we were not sure if these streaks were really heterozygotes but we scored them to be conservative.

We also doubt that the 100 allele for Gpi-1 is really present in the *Littorina* sp. population at Tatoosh; an allele with a frequency of 0.01 would be expected to be present almost exclusively in heterozygotes (see DOBZHANSKY *et al.*, 1977); yet we never saw the clear three banded pattern for any *L. sp.* individual that we saw in *L. scutulata* heterozygotes for Gpi-1.

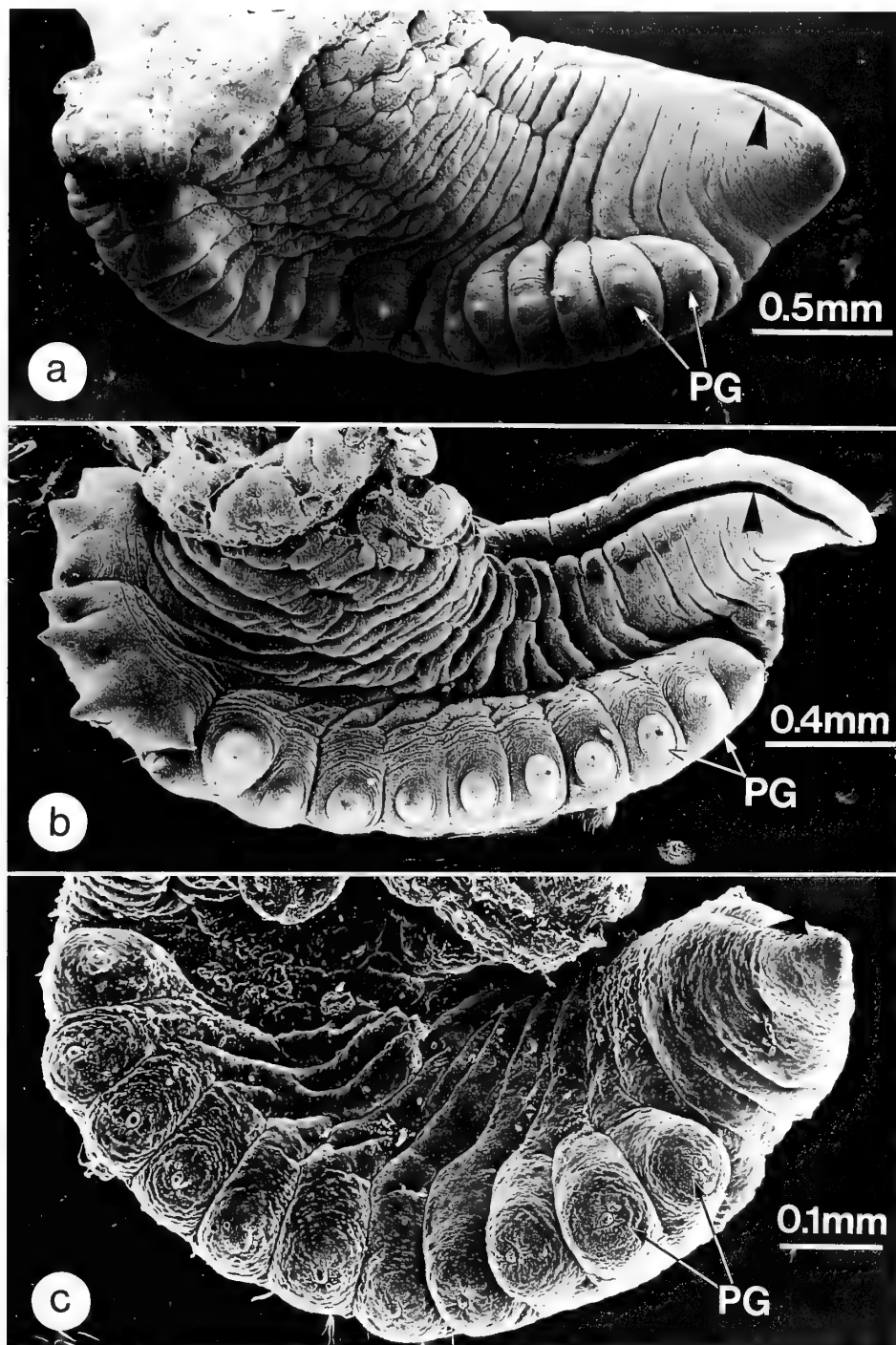


Figure 3

Scanning electron micrograph (SEM) of penes of three taxa (*Littorina*) showing number and arrangement of penial glands (PG). Arrowheads indicate dorsal sperm groove. a. *L. "kurila"*, b. *L. sitkana*, and c. *L. sp.*

There was a rare allele slower than the 100 allele at the 6-Pgd locus that was present for *Littorina* sp. and not for *L. sitkana*, and another rare allele slower than the 100 allele at the Pep-2 locus that was present for *L. sp.* but not for *L. sitkana*.

The value of Nei's unbiased genetic identity obtained for *Littorina sitkana* and *L. sp.* was 0.63 for the 10 loci assayed for all OTUs (Table 8). Four loci—Sod-S, Sod-F, Mdh-S, and Lap-S—were observed to be monomorphic for both *L. sitkana* and *L. sp.* These data were included

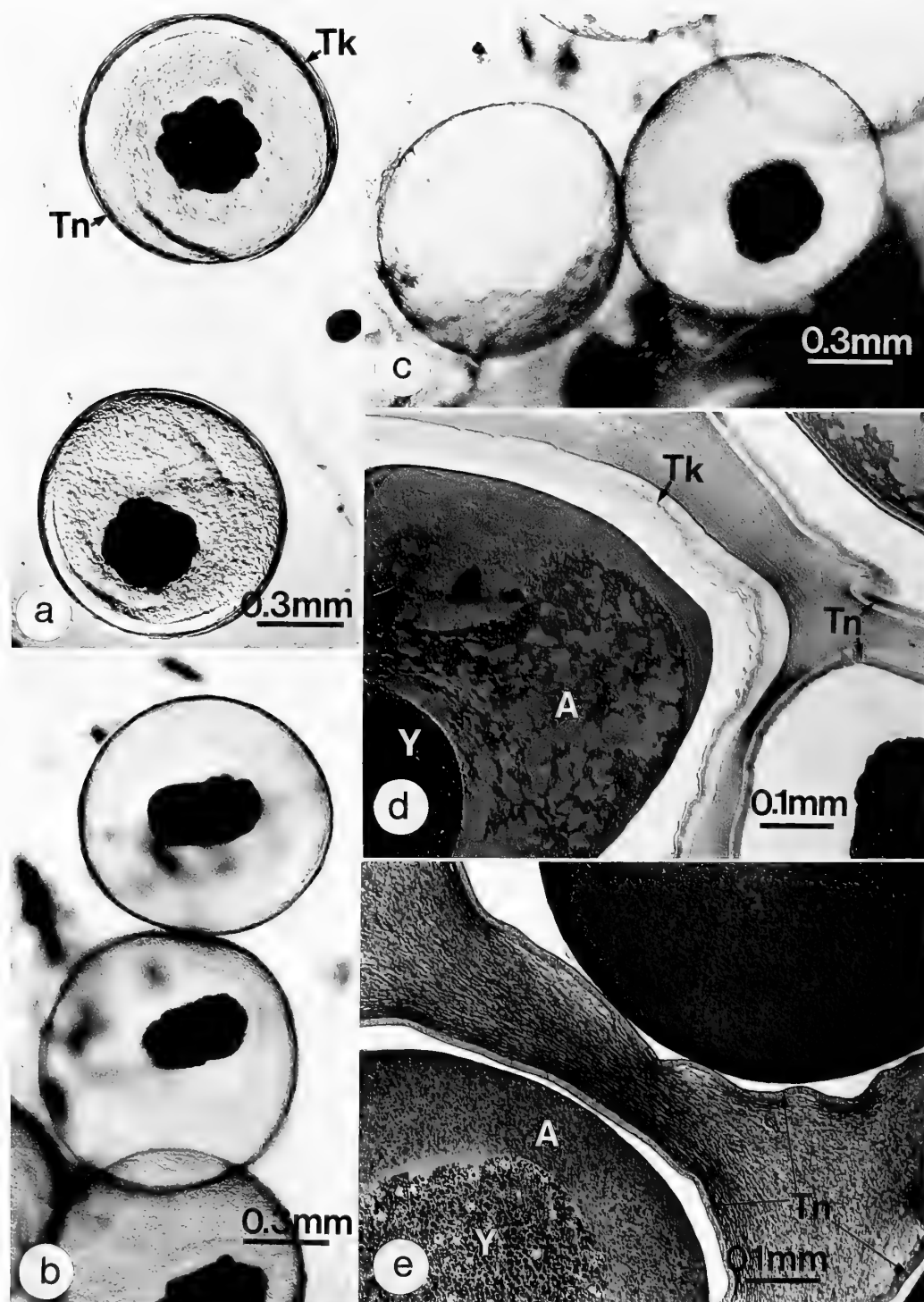


Figure 4

Egg capsule morphology of the three taxa (*Littorina*). All eggs were laid at Friday Harbor Laboratories. a. Two egg capsules of *L. sitkana* from Tatoosh Island each containing an embryo. Tk indicates thick side of capsule and Tn indicates thin side. b. Egg capsule of uniform thickness of *L. sp.* from Tatoosh Island. c. Egg capsules of uniform thickness of *L. "kurila"* from Adak. d. Light micrograph of a $1\ \mu\text{m}$ section through an egg mass of *L. sitkana* viewed with Nomarski optics. Note that egg capsule wall has a thick side (Tk) and a thin side (Tn). Y marks the yolk and A marks the albumen, which is patchy and has shrunk back from the egg capsule wall. The dark region between the capsules is the jelly matrix in which the capsules are embedded. e. Light micrograph of $1\ \mu\text{m}$ section through an egg mass of *L. sp.* Note thin capsule wall relative to d.

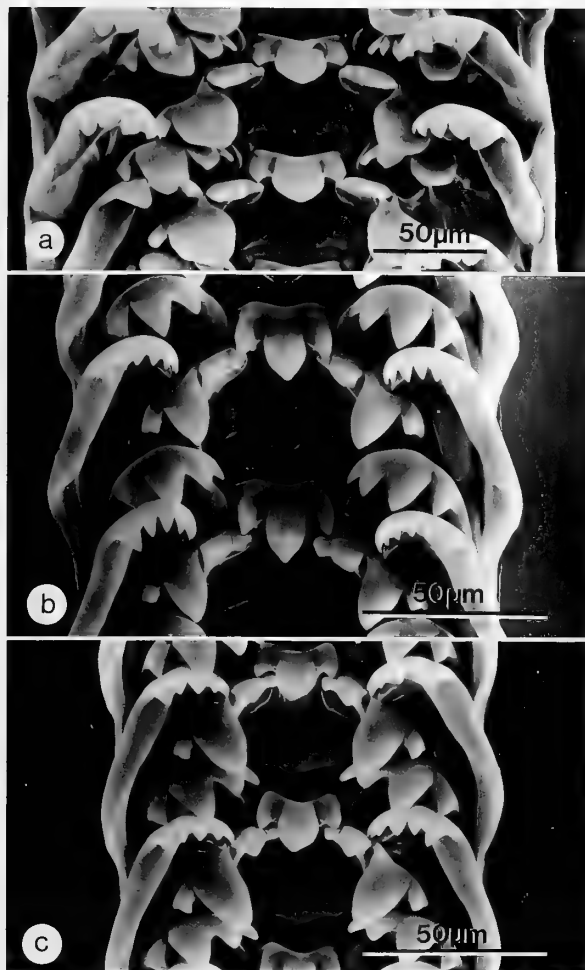


Figure 5

SEM of radulas of the three *Littorina* species. a. *L. "kurila,"* b. *L. sitkana*, c. *L. sp.* Note that the central tooth (rachidian) is narrowest and most pointed in *L. sitkana*, intermediate in *L. sp.* and most blunt in *L. "kurila."* The number of cusps on the outer marginal teeth varies from about 6 or 7 for *L. "kurila,"* to 7 or 8 for *L. sp.*, and 9 or 10 for *L. sitkana*.

in a separate run of Biosys-1 making the total number of loci 14; this gave a value of Nei's unbiased genetic identity of 0.74 and a value of Cavalli-Sforza and Edwards' chord distance of 0.46.

The esterase phenotype was also useful in distinguishing *Littorina sitkana* and *L. sp.* (Figure 8a). The Est-3 band was closer to the Est-2 band for the *L. sitkana* than for *L. sp.* The patterns at the darkly staining Est-5 region also were different but were even more difficult to score. The *L. sp.* has some common alleles for the Est-5 region that are faster than any present for *L. sitkana* from Tatoosh (Figure 8a).

Intraspecific relationships: Of the four populations of *Littorina sitkana* surveyed for all 10 loci, the Mukkaw Bay population and the Oregon population were similar to the Tatoosh population in being fixed for the 100 allele at the Gpi-1, Sdh-4, and Pgm-1 loci. These same loci were also fixed for the 100 allele in the Hoonah and Whitestone populations of *L. sitkana* (Table 1). However, the Adak population of *L. sitkana* differs in having about equal numbers of the *Sdh-4*¹⁰⁰ and *Sdh-4*¹⁰⁸ alleles and in being fixed for a faster allele for the Pgm-1 locus (Table 7). The *L. sitkana* population from Oregon was unique in being fixed for a single band in the Est-5 region and at the Est-3 region (Figure 8a) and also in showing no variation at any of the other 10 loci surveyed (Table 7).

The two populations of *Littorina sp.* that were surveyed for all 10 loci (Table 7) and the Shi Shi ($n = 3$) population were similar in being fixed or nearly fixed for *Gpi-1*⁹⁶ allele and the *Sdh-4*¹⁰⁸ allele.

Interspecific relationships: *Littorina littorea* and *L. obtusata* were the most different from the other *Littorina* OTUs (Table 7). All the *Littorina* OTUs were fixed for the 100 alleles at the β -Gala and β -Ga loci except for *L. obtusata*. *Littorina littorea* and *L. scutulata* had unique alleles at the Pgm-1 locus. *Littorina scutulata* had unique alleles at the Sdh-4 locus that were not shared by any of the other OTUs. All the *Littorina* OTUs were fixed or

Table 6

Results of attempted crosses between *Littorina sitkana* and *L. sp.* from different populations. Only fertile eggs produced between 31 August 1988 and 31 August 1989 are noted. All females were virgin when confined with the male. Fractions refer to number of crosses producing fertile eggs out of number of crosses attempted.

Female species	Male species		<i>L. sp.</i>	<i>L. sitkana</i>				
	Site ¹ :	Site	Tatoosh	Tatoosh	Adak	Siletz	Attu	Hoonah
<i>L. sp.</i>		Tatoosh	19/20 ²	0/2 ²				
<i>L. sitkana</i>		Tatoosh	0/4 ²	4/4	1/2		4/4	1/1
<i>L. sitkana</i>		Adak		1/2	2/6	1/3		
<i>L. sitkana</i>		Siletz		2/5		2/4	2/4	2/3
<i>L. sitkana</i>		Attu						
<i>L. sitkāna</i>		Hoonah		3/4				2/2

¹ Site locations are specified in Table 1.

² See text for more information.

Table 7
Allele frequencies in *Littorina* populations sampled.

	Population ¹													
	si Ta	si Al	si Mk	si OR	sax RI	ob RI	sp Ta	sp Ba	ku Al	sub Mk	sub Gh	lit RI	sc Ta	Lac Fh
Locus														
6-Pgd														
(n)	12	3	3	3	10	16	18	5	6	5	12	11	7	4
88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00
92	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100	1.00	1.00	1.00	1.00	0.85	1.00	0.97	1.00	1.00	1.00	1.00	0.27	0.93	0.00
104	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
112	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
114	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
122	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Pep-3														
(n)	27	10	3	2	20	23	26	5	5	13	12	20	17	6
96	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
98	0.00	0.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	0.04	0.00	0.00	0.00	0.00
100	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.96	1.00	0.00	1.00	0.00
104	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Pep-2														
(n)	48	3	12	12	30	29	60	6	15	26	10	12	55	4
60	0.00	0.00	0.042	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
92	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100	1.00	1.00	0.96	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	0.97	0.00
106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.37	1.00
Gpi-1														
(n)	116	10	10	32	24	26	43	6	22	19	21	29	56	4
86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
92	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
94	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00
96	0.00	0.00	0.00	0.00	0.04	0.77	0.98	1.00	1.00	1.00	1.00	0.00	0.00	0.00
100	1.00	1.00	1.00	1.00	0.96	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
106	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
112	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.75
Aat-1														
(n)	43	6	3	19	12	10	39	3	13	5	3	8	38	4
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
108	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
β-Gala														
(n)	15	4	1	3	16	17	17	6	5	9	14	17	12	3
100	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
108	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
130	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
β-Ga														
(n)	20	6	3	3	21	15	25	6	7	12	17	16	12	4
100	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
112	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
116	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Sdh-4														
(n)	67	10	7	38	22	11	22	5	21	25	12	21	50	3
100	0.96	0.45	1.00	1.00	0.16	0.00	0.02	0.00	0.00	0.00	0.17	1.00	0.00	0.00
108	0.04	0.55	0.00	0.00	0.84	1.00	0.98	1.00	1.00	1.00	0.83	0.00	0.00	0.00
114	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00

Table 7
Continued.

	Population ¹													
	si Ta	si Al	si Mk	si OR	sax RI	ob RI	sp Ta	sp Ba	ku Al	sub Mk	sub Gh	lit RI	sc Ta	Lac Fh
120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.00
124	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
126	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00
130	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67
Sdh-1														
(n)	14	10	2	2	36	37	18	2	4	2	2	22	30	0
100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—
Pgm-1														
(n)	7	11	14	3	30	29	40	10	12	26	25	30	18	8
74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.50	0.00
86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00
94	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
96	0.00	0.00	0.00	0.00	0.03	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
98	0.00	0.00	0.00	0.00	0.97	0.65	0.60	1.00	0.00	0.61	0.76	0.00	0.00	0.13
100	1.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
102	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.58	0.27	0.12	0.00	0.00	0.87
104	0.00	1.00	0.00	0.00	0.00	0.00	0.05	0.00	0.42	0.12	0.12	0.00	0.00	0.00

¹ Key to populations: si Ta = *L. sitkana* Tatoosh; si Al = *L. sitkana* Aleutian Is.; si Mk = *L. sitkana* Mukkaw; si OR = *L. sitkana* Oregon; sax RI = *L. saxatilis* Rhode Is.; ob RI = *L. obtusata* Rhode Is.; sp Ta = *L. sp.* Tatoosh; sp BA = *L. sp.* Bamfield; ku Al = *L. "kurila"* Aleutian Is.; sub Mk = *L. subrotundata* Mukkaw; sub Gh = *L. subrotundata* Grays Harbor; lit RI = *L. littorea* Rhode Is.; sc Ta = *L. scutulata* Tatoosh; Lac Fh = *Lacuna* Friday Harbor.

nearly fixed for the 100 allele at the 6-Pdg locus, whereas *L. littorea* had only a low frequency of the 100 allele.

Lacuna was too distantly related to be a good outgroup; it shared alleles with other OTUs only at the Pep-2 locus (with *Littorina scutulata*), and the Gpi-1 locus (with *Littorina littorea*), and at the Pgm-1 locus (with the *Littorina subrotundata*) (Table 7). Therefore we used *Littorina littorea* as an outgroup for our analysis even though BOULDING (1990b) had previously used *Lacuna* as the outgroup.

The distance-Wagner tree constructed using CAVALI-SFORZA & EDWARDS' (1967) chord distance is shown in Figure 9. For all species the absolute distances of the OTUs from the root varied considerably under different bootstrap runs. *Littorina scutulata* was consistently distant from all other OTUs and consistently branched off the phylogeny just after *L. littorea*. *Littorina obtusata* was consistently distant from all other OTUs and especially distant from *L. littorea*, but its position of attachment onto the phylogeny was not robust under bootstrapping.

There was a cluster made up of *Littorina sitkana* populations from Tatoosh, Mukkaw, and Oregon that was robust under the bootstrapping. The *L. subrotundata* from Grays Harbor and from Mukkaw Bay often formed a distinct cluster but sometimes clustered with *L. sp.* and *L. "kurila."* The *L. sp.* from Bamfield and from Tatoosh clustered together most of the time but often *L. saxatilis* or *L. subrotundata* moved into the cluster.

The *Littorina sitkana* from Adak Island in the Aleutians shared alleles with the *L. sitkana* cluster and also with the *L. sp.* cluster.

The *Littorina subrotundata* from Mukkaw and the *L. subrotundata* from Grays Harbor did not form a group that was significantly distinct from the *L. sp.* from Tatoosh and Bamfield. *Littorina subrotundata* from both locations were fixed for the 100 allele while *L. sp.* was fixed for the 98 allele at the Pep-3 locus (Table 7). We scored one 98 allele in one *L. subrotundata* individual near the edge of the gel but we think this is an error. The 98 and 100 alleles of Pep-3 were a maximum of 2 mm apart so they could not be distinguished on some gels and were not distinguished in BOULDING (1990b). We eliminated all the Pep-3 data from any gel that was not run long enough to distinguish the 98 and 100 alleles. This resulted in smaller sample sizes for this locus but enabled us to include data from these alleles (Table 7). These two alleles could be distinguished more consistently in future studies if the gels were run longer or perhaps by changing the pH of the buffer.

Littorina saxatilis and *L. sp.* could be distinguished by a nearly fixed difference at the Gpi-1 locus (Table 7). They also had different allele frequencies and some unique alleles at the Sdh-4 and Pgm-1 loci (Table 7).

Nei's genetic identity for *Littorina sp.* from Tatoosh and *L. "kurila"* from Adak is 0.971 (Table 8) for the 10 loci assayed for all OTUs. Most of the difference is at the

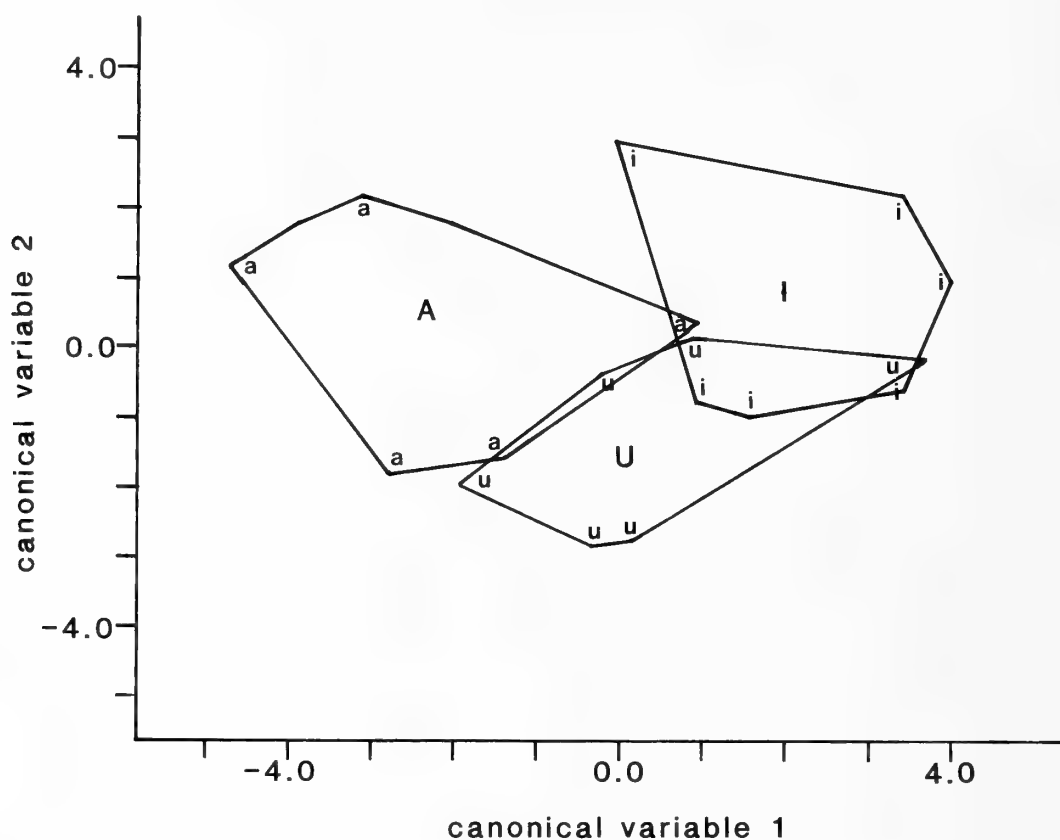


Figure 6

Plot of the first canonical variable (CV1) against the second canonical variable (CV2) for the first discriminant with adult snails (*Littorina*) collected from the field only. Centroids for each group are as follows: U = *L. "kurila"* from Adak Island, I = *L. sitkana* from Tatoosh Island, and A = *L. sp.* from Tatoosh Island. Outlines are convex hulls (curves) surrounding 100% of the points for that group.

Pgm-1 locus complex where the two taxa have a single locus Nei's genetic identity of 0.417.

DISCUSSION

Morphometrics

An important finding of this study is that the *Littorina* sp. from the sparse treatment, cultured at a density of 10 juveniles per dish, differed more in shell shape from the *L. sp.* in the dense treatment, cultured at a density of 30 juveniles per dish, than any of the three species differed from each other. This is even more surprising considering that each dish in the sparse treatment was paired with a dish of full siblings in the dense treatment, so the genetic diversity between these two groups was much less than between any other two groups in the analysis. This shows clearly that multivariate morphometric analyses alone do not solve the taxonomic problems of sibling species. Workers on littorinids and other gastropods should be cautious about interpreting separation on a multivariate plot as evidence for or against the existence of a sibling species (*e.g.*, MURRAY, 1982; WELLINGTON & KURIS, 1983; JANSON

& SUNDBERG, 1983; JANSON, 1985; JANSON & WARD, 1985).

It is important to distinguish differences in size from differences in shape in order to identify the shells of juvenile littorinids from closely related taxa. Ratios of shell measurements to shell lengths are used commonly in species descriptions and were used by RAUP (1961, 1966) in his theoretical models of shell shape, but single ratios are not as powerful as multivariate analyses for separating sibling species (PIMENTAL, 1979; REYMENT *et al.*, 1984). A ratio will not be constant within a group if there is allometry (REYMENT *et al.*, 1984) or if there is substantial plasticity. Our data show that the ratio of various shell dimensions to shell length can vary considerably with growth rate (Table 3).

Canonical variate analysis selects coefficients and variables so that a linear combination of the variables is formed that best separates the groups (PIMENTAL, 1979; REYMENT *et al.*, 1984). A problem with canonical variate analysis is that it tends to separate well separated groups further without separating poorly defined groups included in the same analysis. The three field treatments were better sep-

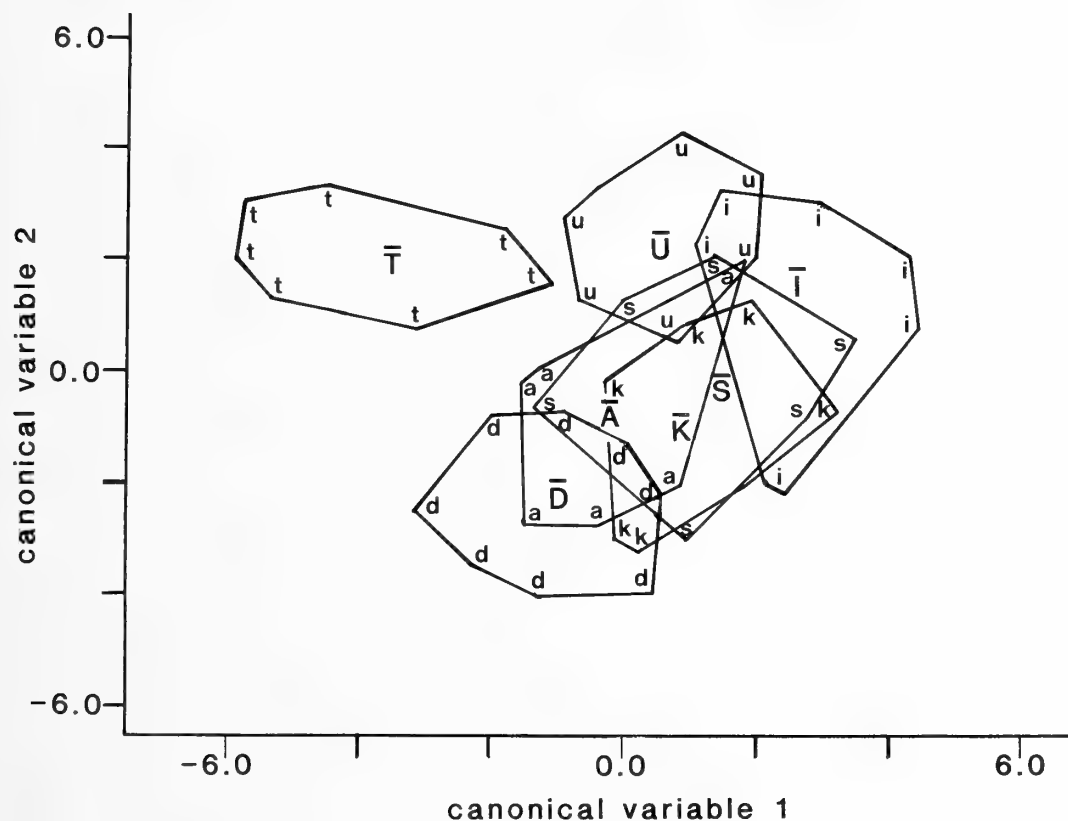


Figure 7

Plot of CV1 against CV2 for the canonical variate analysis from the second discriminant with all seven treatments with *Littorina* species. Centroids for each group are as follows: U = field *L. "kurila,"* K = dish *L. "kurila,"* I = field *L. sitkana,* S = tanks *L. sitkana,* A = field *L. sp.,* T = sparse *L. sp.,* D = dense *L. sp.* Outlines are convex hulls (curves) surrounding 100% of the points for that group.

arated along the axis of CV1 in the first discriminant analysis (Figure 6) than in the second discriminant analysis with all seven groups (Figure 7). The classification functions from this first analysis (Table 4) would be most useful to other workers trying to classify shells collected from the field on the basis of shape alone.

None of the separation along the axes of the canonical variables seemed solely attributable to size (Figures 6, 7, Tables 3–5). This was fortunate because differences in adult size will not be helpful in separating juveniles of these littorinids. SUNDBERG (1988) found that the major part of the variation in shell morphology between exposed and sheltered populations of *Littorina saxatilis* could be attributed to differences in size. What is of considerable interest is whether there is allometry that could result in shape differences among different populations solely due to differences in mean size (K. Johannesson, personal communication). An example of this occurred when shape differences among two stocks of haddock on a canonical variable plot were attributable to differences in mean body size between the two samples (McGLADE & BOULDING, 1983) which probably resulted from fish of similar ages schooling together.

Variation between species of littorinids must be considered in the context of variation within a species, especially in species that have direct development and therefore limited dispersal. JANSON & WARD (1984) studied microgeographical variation in allozyme and shell characters in *Littorina saxatilis*. They found considerable morphological variation within one kilometer, especially between exposed and sheltered populations, but analysis of the allozyme data suggested this was due to within-species variation. In the northeastern Pacific, *L. sitkana* inhabits protected shores and *L. sp.* very exposed shores, but the species co-occur in areas of intermediate exposure near very exposed areas (Boulding & Van Alstyne, in review); it would be interesting to look for microgeographic variation of the sort described by JANSON & WARD (1984) within each of these two species.

Plasticity in Phenotype

Phenotypic plasticity in shell form has long been recognized by gastropod systematists. For example CARPENTER (1864:531) synonymized three species of *Littorina* because he found no gaps in shell form in a large series

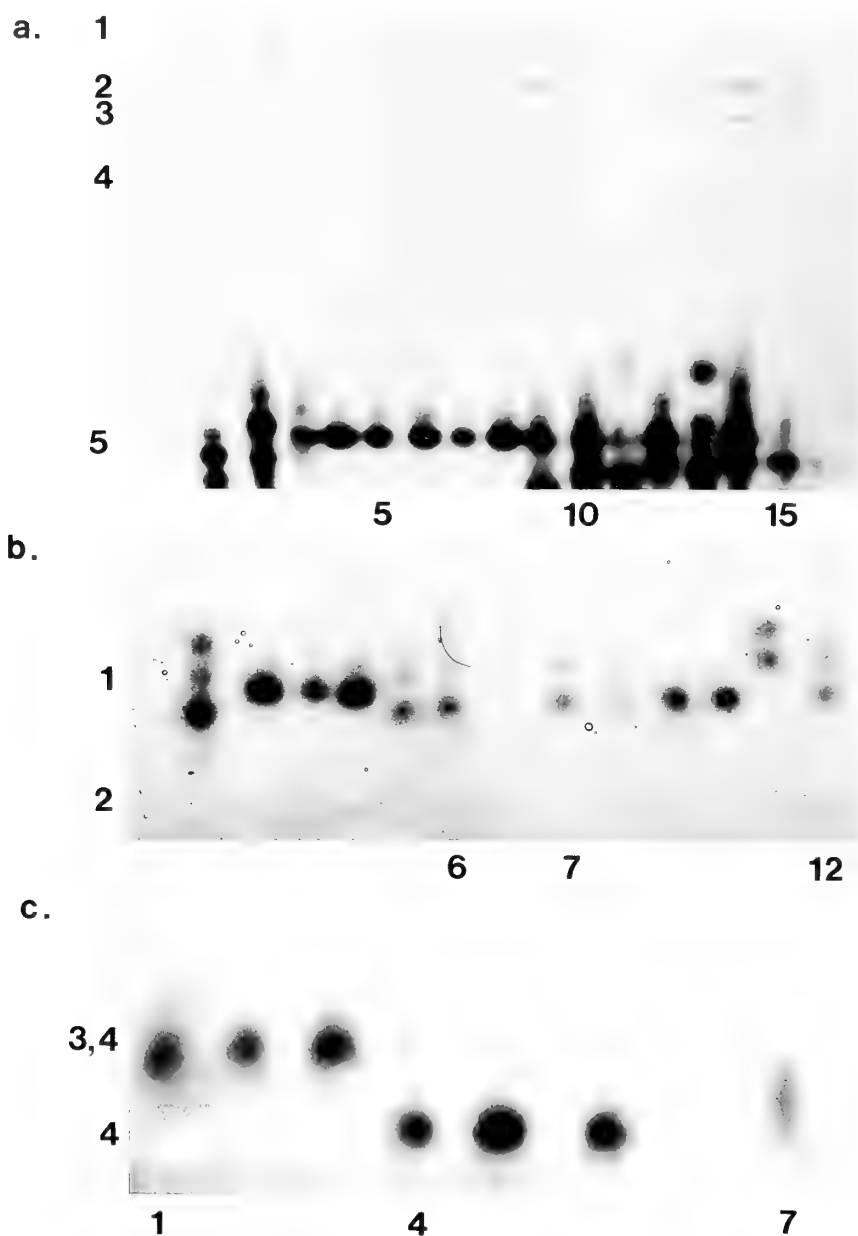


Figure 8

a. A photograph of a gel stained for Est α NA. Lane 1 is *Littorina sitkana* from False Bay, lanes 2 and 3 are *L. scutulata* from Tatoosh, lanes 4 through 8 are *L. sitkana* from Oregon, and lanes 9 through 15 are *L. sp.* from Tatoosh. Note fixed position of bands for *L. sitkana* from Siletz Bay, Oregon. These were fixed for all 30 snails that were assayed from this population, which is near the southern limit for *L. sitkana*. b. A photograph of a gel run in an AmC 7.0 buffer and stained for Pgm using an agar overlay. Lane 1 is *L. sp.* from Tatoosh, lanes 2 to 4 contain *L. sitkana* from Tatoosh, lanes 5 and 6 contain *L. subrotundata* from Grays Harbor, then there is a blank, and lanes 7 to 12 contain *L. subrotundata* from Grays Harbor. Note the position of the allele for *L. sitkana* between the slow and medium alleles shared by the other two species (see text for interpretation). c. A photograph of a gel stained for SDH. Lanes 1 to 3 are *L. sp.*, lanes 4 to 6 are *L. sitkana*, and lane 7 is *L. saxatilis*. Note there are two loci shown: 3, which stains faintly, and 4, which stains darkly. The allele *Sdh-4*¹⁰⁸ for locus 4 for *L. sp.* covers the allele *Sdh-3*¹⁰⁰ for locus 3, whereas for *L. sitkana* the allele *Sdh-4*¹⁰⁰ for locus 4 is slower than the allele *Sdh-3*¹⁰⁰ for locus 3. Note the streak for *L. saxatilis*, which is probably a heterozygote for *Sdh-4*¹⁰⁰/*Sdh-4*¹⁰⁸.

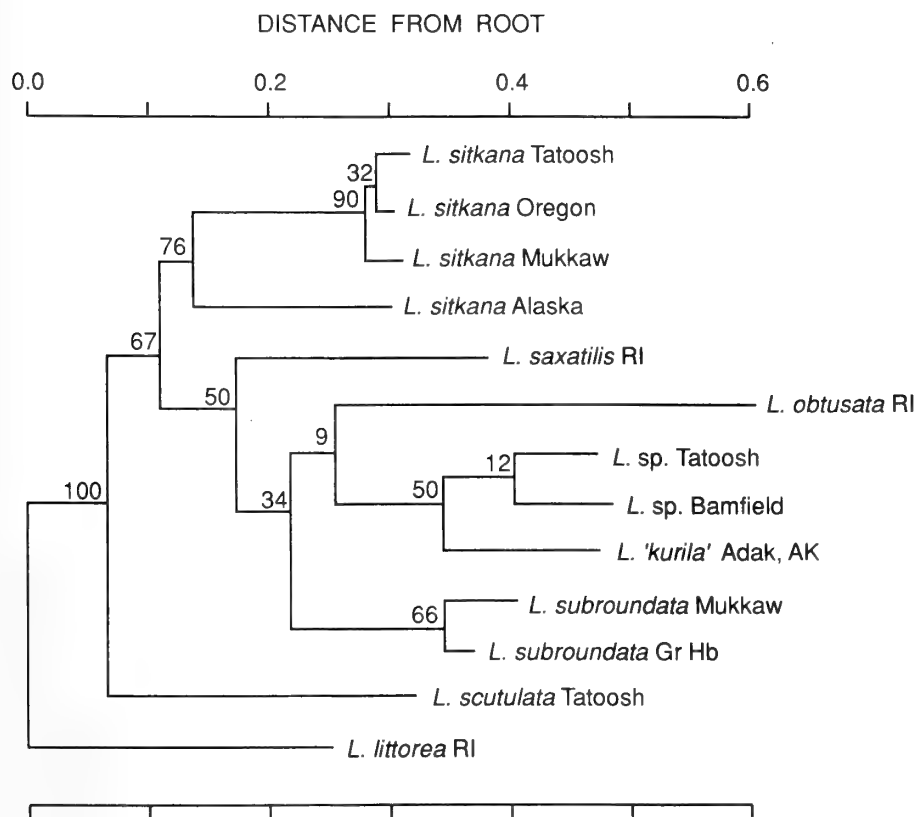


Figure 9

A distance-Wagner tree constructed using CAVALLI-SFORZA & EDWARDS' chord (1967) distance using SWOFFORD's (1981) multiple addition criterion and no optimization. The numbers at the branching points represent the number of times the OTUs to the right of the branch points occurred as a group in the 100 bootstrapped replicates. Distinct for distance-Wagner analysis means that the distance between the groups of OTUs was at least twice that between any two OTUs in the group.

Table 8

Genetic distance measures between pairs of *Littorina* populations. Below diagonal: NEI's (1978) unbiased genetic identity. Above diagonal: CAVALLI-SFORZA & EDWARDS' (1967) chord distance used to construct distance-Wagner tree.

Population ¹	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>L. sitkana</i> Ta	—	0.312	0.057	0.039	0.453	0.674	0.540	0.555	0.555	0.479	0.443	0.532	0.497
2 <i>L. sitkana</i> Al	0.871	—	0.331	0.328	0.418	0.641	0.482	0.514	0.460	0.396	0.372	0.555	0.497
3 <i>L. sitkana</i> Mk	1.000	0.867	—	0.041	0.470	0.687	0.555	0.571	0.571	0.496	0.460	0.533	0.499
4 <i>L. sitkana</i> OR	1.000	0.868	1.000	—	0.468	0.686	0.554	0.569	0.569	0.495	0.458	0.531	0.497
5 <i>L. saxatilis</i> RI	0.728	0.782	0.721	0.722	—	0.561	0.294	0.281	0.398	0.402	0.404	0.578	0.578
6 <i>L. obtusata</i> RI	0.427	0.492	0.419	0.422	0.585	—	0.534	0.518	0.578	0.532	0.533	0.725	0.679
7 <i>L. sp.</i> Ta	0.627	0.700	0.620	0.621	0.890	0.660	—	0.146	0.196	0.266	0.303	0.595	0.574
8 <i>L. sp.</i> Ba	0.606	0.673	0.598	0.600	0.902	0.671	0.988	—	0.285	0.287	0.314	0.602	0.573
9 <i>L. "kurila"</i> Al	0.622	0.734	0.614	0.616	0.823	0.619	0.971	0.924	—	0.310	0.360	0.602	0.573
10 <i>L. subrotundata</i> Mk	0.725	0.809	0.718	0.719	0.789	0.666	0.902	0.894	0.874	—	0.101	0.602	0.499
11 <i>L. subrotundata</i> Gh	0.748	0.815	0.742	0.743	0.790	0.661	0.888	0.891	0.846	0.996	—	0.574	0.497
12 <i>L. littorea</i> RI	0.655	0.615	0.655	0.656	0.585	0.358	0.572	0.552	0.566	0.570	0.590	—	0.577
13 <i>L. scutulata</i> Ta	0.763	0.781	0.759	0.761	0.658	0.464	0.671	0.650	0.668	0.781	0.788	0.622	—

¹ Key to locations: Ta = Tatoosh Island; Al = Adak Island; Mk = Mukkaw Bay, Washington; OR = Siletz Bay, Oregon; RI = Rhode Island; Ba = Bamfield; Gh = Grays Harbor, Washington. For more information on locations see Table 1.

of specimens. Unfortunately the approach of identifying species by looking for large breaks in an ordered series of forms does not work well for some groups; two of the littorinids that Carpenter synonymized are considered by MURRAY (1979, 1982) and MASTRO *et al.* (1982) to be separate species.

The range of shell shape and shell sculpture in *Littorina* sp. raised at high and low densities, which resulted in low and high growth rates respectively, differs from the range seen in *L. sitkana* cultured at low and high growth rates; this suggests significant genetic differences between the two taxa. No *L. sp.* ever developed deep spiral sculpture characteristic of *L. sitkana* in the field and no *L. sitkana* ever became as high spired as the *L. sp.* grown at low densities in the dishes or in the tanks. In contrast *L. sitkana* grown at fast growth rates tended to have lower spires than those that had grown more slowly.

Soft part anatomy also has been shown to change with ontogeny and with changes in environmental conditions. Foot size of a thaidid gastropod has been shown to vary with environmental conditions (ETTER, 1988). Variation in penial morphology and pigmentation (HANNAFORD ELLIS, 1979; RAFFAELLI, 1979), number of penial glands (RAFFAELLI, 1979; JANSON, 1982), number of cusps on the outer marginal teeth of the radula (REIMCHEN, 1974), bluntness of rachidian teeth of the radula (RAFFAELLI, 1979), and amount of head pigmentation (JAMES, 1968) with size for species in the *Littorina saxatilis* species complex makes it difficult to use these characters to distinguish between sibling species.

Penial morphology and the morphology of the bursa copulatrix are likely important in species cohesiveness. SAUR (1990) found that initiation of copulation occurred as frequently with same sex partners as with those of the opposite sex but that the duration of copulation was considerably shorter for intrasexual copulation. She hypothesizes that sex and species recognition occurs when the penis contacts the bursa copulatrix and that this recognition prolongs copulation. We do not know whether the small differences in penial morphology between *Littorina sitkana* and *L. sp.* (Figure 3) are significant for species recognition or whether it is the secretions from the penial glands that are important.

Hybridization and Speciation

The ability of *Littorina sitkana* from the north and south extremes of the species distribution to interbreed supports the classification of *L. sitkana* as one species in the northern Pacific. However, the viability and fertility of the hybrid offspring and their ability to backcross with their parents would have to be tested before this could be shown conclusively. WARWICK *et al.* (1990) have reported that while male *L. saxatilis* could be crossed with female *L. arcana*, the reverse was not true; the female hybrid progeny could be backcrossed to male *L. saxatilis*. There are many documented cases where male hybrid inviability or sterility

develops during the speciation process before female hybrid inviability or sterility (for review see DOBZHANSKY *et al.*, 1977; COYNE & ORR, 1989). So far we have been unable to obtain a single offspring from the many reciprocal *L. sitkana* × *L. sp.* crosses or the few *L. sp.* female × *L. "kurila"* male crosses we have tried. Even if we were to obtain *L. sp.* × *L. "kurila"* hybrids we would have to check the fertility of both the male and female hybrid offspring before we concluded they were capable of interbreeding. One factor that makes crossing the latter two taxa difficult is that the *L. "kurila"* from Adak lays eggs only once a year, in late June to early July, whereas *L. sp.* lays eggs all year round. This could be the result of a cline in the timing of onset of reproduction; GOLIKOV & KUSSAKIN (1978) report that the onset of reproduction becomes later in the summer for *L. kurila* from the northwestern Pacific and BEHRENS YAMADA (1989) reports that *L. sitkana* from Oregon had different periods of peak reproduction than *L. sitkana* from Friday Harbor.

Biochemical Systematics

Allozyme differences among *Littorina sitkana*, *L. sp.*, *L. "kurila"*, and *L. subrotundata*: Our electrophoretic data show clearly that *Littorina sitkana* and *L. sp.* are two distinct species. There are fixed or nearly fixed differences in allelic allozymes at four loci (Table 7). The presence of fixed differences in allelic allozymes between sympatric populations is strong evidence that the populations are reproductively isolated (FERGUSON, 1980). These two species are sympatric on Tatoosh Island—their distributions overlap in areas of intermediate exposure (Boulding & Van Alstyne, unpublished data) and they have the opportunity to interbreed. But *L. sp.* is abundant only on extremely wave-exposed intertidal shores while *L. sitkana* is abundant only on protected shores (Boulding & Van Alstyne, unpublished data).

Before interpreting unique bands on a gel as evidence of absence of gene flow between two sympatric taxa, the genetic basis of the banding pattern should first be established (FERGUSON, 1980). WARD *et al.* (1986, 1991) have done breeding studies to confirm the Mendelian segregation of codominant alleles for the enzyme loci Gpi, Aat-1, Pgm-1, Pgm-2, and for 10 other loci for *Littorina saxatilis*. DILLON (1986) demonstrated that Gpi, Opdh, and Est showed Mendelian inheritance patterns for the freshwater snail *Goniobasis proxima* when held under standard conditions.

These results from electrophoresis of allozymes support our conclusion from the morphological data that *Littorina* sp. is not conspecific with *L. sitkana*. Two populations of *L. subrotundata* were fixed for *Pep-3*¹⁰⁰ and two populations of *L. sp.* were fixed for *Pep-3*⁹⁸, which suggests they are separate taxa; this result would be more conclusive if we had sampled more populations.

In contrast, the differences in allele frequencies between *Littorina* sp. from Tatoosh and *L. "kurila"* from Adak

Island in the Aleutians might result from a geographical cline in allele frequencies (see DOBZHANSKY *et al.*, 1977) and does not necessarily mean they should be considered different species. Microgeographic clines are also known; JOHANNESSON & JOHANNESSON (1989) found a cline in the allele frequency of Aat between high- and mid-rocky shore populations of *L. saxatilis*.

Littorina sitkana from Adak was more similar to *L. "kurila"* from Adak (Nei's genetic identity = 0.73) than *L. sitkana* from Tatoosh was to *L. sp.* from Tatoosh ($I = 0.63$ for same 10 loci).

Interspecific relationships: In some cases phylogenies from allozyme data can provide better resolution than those constructed using newer techniques such as restriction enzyme analysis of mtDNA (DOWLING & BROWN, 1989) although the best resolution may come from direct sequencing of DNA using the polymerase chain reaction (INNIS *et al.*, 1988). Considerable literature has been devoted to the merits of one method of constructing phylogenies from distance data over another (see FELSENSTEIN, 1982; ROGERS, 1986). However, the subsets of OTUs that were robust under the bootstrapping were almost the same for a UPGMA dendrogram we constructed but do not present (BOULDING, 1990b) and the distance-Wagner tree we do present (Figure 9). Both trees showed one subset consisting of *Littorina sitkana* from Tatoosh, Mukkaw Bay, and Oregon and a second less robust subset consisting of *L. sp.* from Bamfield and Tatoosh and *L. "kurila"* from Adak. *Littorina scutulata*, *L. obtusata*, and *L. littorea* were only distantly related to the two clusters and to each other.

The quality of phylogenies at the species level based on allozyme data depends mostly on the number of loci surveyed and is less dependent on the sample size drawn from each population (FERGUSON, 1980). This is because in interspecific comparisons loci are usually either fixed for different allelic allozymes or identical making it unnecessary to estimate precisely allele frequencies (AVISE, 1983). Only 10 loci were used in the present study, which allowed resolution of parts of the phylogeny dealing with more distantly related species but did not allow us to determine the exact branching pattern for more closely related species.

We encountered problems with using bootstrapping to put confidence limits on our trees based on allozyme data. Two of our enzyme loci, Aat-1 and Sdh-1, were monomorphic for all species that were included in the analysis (Table 7). The replicate bootstrap samples that happened to get several copies of these monomorphic loci contributed to the low scores at several of the branch points (Figure 9). This was particularly true for branch points between species such as *Littorina subrotundata* and *L. sp.* These were different at only the Pep-3 locus, which is a digestive enzyme. The bootstrapping procedure treats all loci equally, yet digestive enzymes, such as the esterases and peptidases, accumulate different alleles at a faster rate than enzymes involved in central metabolic processes and are therefore more likely to distinguish closely related species

(see FERGUSON, 1980). Hillis (presentation at SSB meeting, 1991) has created experimental phylogenies using different cultures of a phage and reports that 95% confidence limits determined by bootstrapping DNA sequence data is an overly conservative method of detecting robust groupings of OTUs; he says that groupings that appear together 70% of the time should be considered robust.

Comparison of phylogenies constructed from allozyme data with those derived from morphological data often reveals similarities and differences (HILLIS, 1987). The species of littorinids used in this study have been included in a phylogeny based on morphological characters (REID, 1990). Reid's phylogeny shows *Littorina scutulata* branching off the cladogram, then *L. littorea*, then *L. sitkana*, then *L. "kurila"*, then *L. obtusata*, and finally *L. saxatilis*. This pattern is not really as different from the distance-Wagner tree (Figure 9) as first appears. If only the robust branches of Figure 9 are considered, then the branching order is really only significantly different for *L. obtusata*, which may be more distinct from the *L. sitkana* cluster and the *L. sp.* cluster than is indicated by Reid. The position of *L. saxatilis* on our phylogeny is not resolved by our allozyme data although the data show *L. saxatilis* is a separate taxon from *L. sitkana* and from *L. sp.*

Systematics of *Littorina sitkana*, *L. sp.*, and *L. "kurila"*

The differences in shell shape, shell weight and ridging under different growth conditions, head and penis pigmentation, egg capsule and spawn morphology, and size at maturity demonstrate that *Littorina sitkana* and *L. sp.* are separate species. Their failure to hybridize supports this conclusion. The electrophoretic data showed that these two species are fixed or almost fixed for different alleles at four loci, Pgm-1, Gpi-1, Pep-3 and Sdh-4, and that they have different banding patterns for Est α NA.

If only field-collected adult snails from three taxa are considered, then additional snails from these populations could be assigned to a taxon with a reliability of about 90% using our discriminant function on their shell shape measurements. Of course if data on shell ridging or soft part pigmentation were included, the reliability would be much higher. The use of the field characters described here has made it possible to tell the two species apart 100% of the time.

Littorina sp. shows a number of genetic differences from *L. "kurila"* in the light pigmentation of its head, its unpigmented penis, and in the timing of its reproductive period, and may be a separate taxon. The differences in pigmentation were heritable. We observed differences in behaviors adapting *L. sp.* to wave-exposed habitats, such as its rapid emergence from its shell when dislodged and its rapid subsequent readhesion to the substrate (Boulding & Van Alstyne, unpublished data), not seen in the *L. "kurila"* collected from Adak or in their offspring cultured at Friday Harbor Laboratories. Alternatively *L. "kurila"*

and *L. sp.* may represent the north and south ends of a geographic cline. Only more extensive collections from Alaska and the Aleutian islands can resolve whether *L. "kurila"* and *L. sp.* are separate species.

REID & GOLIKOV (1991) and REID *et al.* (1991) have described some new species of *Littorina* from the northwestern Pacific. They have found the form of the pallial oviduct to be a useful taxonomic character. We agree that the form of the oviduct can be useful and we agree with Reid that there is a close relationship among *L. subrotundata*, *L. "kurila"*, and *L. sp.* and a more distant relationship between these taxa and *L. sitkana*. What is less certain is whether it is advisable for REID & GOLIKOV (1991) to synonymize *L. "kurila"*, *L. sp.*, and *L. subrotundata* into *L. subrotundata*, because they found no significant differences in the pallial oviduct or other anatomical characters. We think the fixed differences at the Pep-3 locus for two populations of *L. sp.* and of *L. subrotundata* make it unlikely these two taxa are conspecific. While direct development can result in increased microgeographic differentiation within a taxon (*e.g.*, JANSON & WARD, 1984), it may also promote speciation because of the reduced levels of gene flow (see BOULDING, 1990).

The divergence between *Littorina "kurila"* and *L. sitkana* may have resulted as they moved south and encountered opposing selective pressures on exposed and protected shores (BOULDING, 1990a) and may have resulted in the exposed-shore species *L. sp.* *Littorina sp.* and *L. "kurila"* are thin-shelled and would be unlikely to persist where crabs were abundant (Boulding & Van Alstyne, unpublished data). No intertidal, shell-breaking crabs were observed on Adak Island where *L. sitkana* and *L. "kurila"* were collected (G. J. Vermeij, personal communication). In contrast, the thick shell of *L. sitkana* makes it resistant to predation by shore crabs (Boulding & Van Alstyne, unpublished data; Behrens Yamada & Boulding, unpublished data) which are abundant on protected shores in the northeastern Pacific.

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A New *Ashmunella* (Gastropoda: Pulmonata: Polygyridae) from Sonora, Mexico

by

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Abstract. A new species of *Ashmunella* is described from near Cananea in Sonora, Mexico, and comparisons are made with the closely related Chiricahuan species.

INTRODUCTION

This paper describing a new species of *Ashmunella* is part of a continuing study of the morphology and systematics of members of this genus. For comparative material I have relied heavily on the collection of Walter B. Miller as well as personal collections over the last 22 years.

Ashmunella milesi Reeder, sp. nov.

(Figures 1–5)

Diagnosis: A medium-sized, depressed *Ashmunella* with a tridentate aperture and having an additional parietal callous in about 50% of the individuals; with the upper chamber of the bipartite penis narrower and longer than the lower chamber; with relatively long epiphallus and short epiphallic caecum.

Description of shell of holotype: Shell (Figures 1–3) of moderate size, depressed, lenticulate with relatively sharp shoulder and with open umbilicus, umbilicus contained about 6.0 times in the diameter of the shell. Color pale brown. Aperture with lip sharply reflexed, narrow, having two narrow basal teeth and a single, broader palatal tooth. Parietal wall with a prominent tooth and a smaller callous above the main tooth lying somewhat deeper within the aperture. Embryonic shell smooth with postembryonic whorls showing faint radially arranged bumps with numerous spirally arranged incised lines, the latter becoming prominent on the body whorl both above the periphery and on base of shell. Prominent radial growth ridges on all major whorls.

Diameter 13.5 mm, height 6.2 mm, umbilicus 2.3 mm, number of whorls 6.5.

Reproductive anatomy of holotype: The genitalia (Fig-

ure 5) are typical of the genus, with a bipartite penis, a relatively long epiphallus, and a short epiphallic caecum. The penial retractor inserts on the epiphallus. The spermatheca is long and tubular without a terminal enlargement. Upper chamber of penis is about 2.5 times as long as the lower chamber from which it is sharply demarcated; lower chamber is considerably broader than the upper. Measurements of genital structures are as follows:

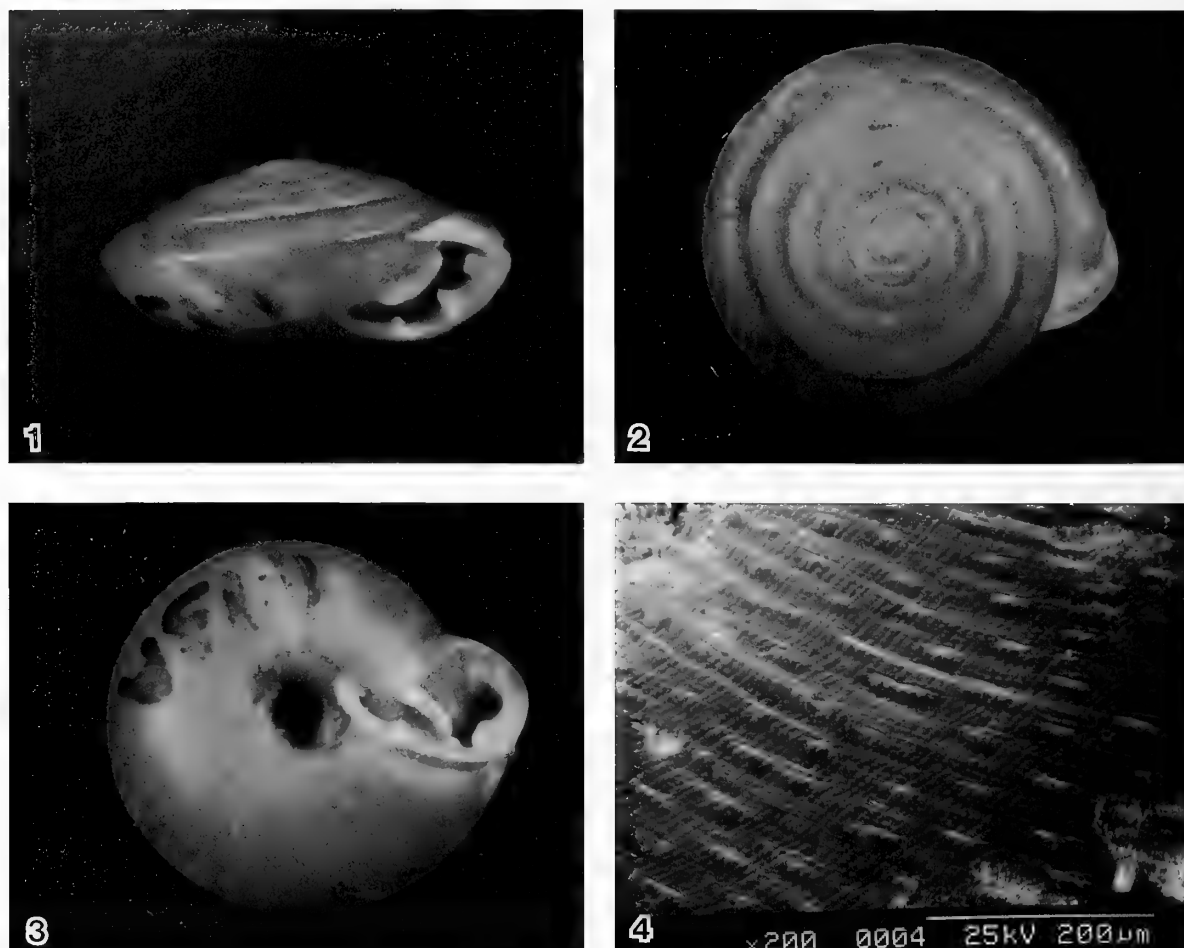
lower penis	2.0 mm
upper penis	5.4 mm
epiphallus	14.0 mm
epiphallic caecum	2.4 mm
spermatheca	19.6 mm

Variations in paratypes: A total of 39 adult shells was examined. These ranged in diameter from 12.1 mm to 13.6 mm with an average of 12.85 mm. The height ranged from 5.1 mm to 6.5 mm with an average of 5.95 mm. All of the unworn specimens exhibited the characteristic radial growth ridges and impressed spiral lines, and most exhibited elongate pustules (Figure 4). A total of 19 of the shells exhibited the extra parietal callous to some degree.

Description of types: Holotype: Santa Barbara Museum of Natural History No. 35609. Paratypes: The Academy of Natural Sciences of Philadelphia No. 392397; U.S. National Museum No. 860573; collections of C. D. Miles, W. B. Miller, and R. L. Reeder.

Type locality: Northern Sonora, Mexico, west of Cananea; south-facing talus slope along road to microwave tower, Sierra Mariquita; 31°2.0'N, 110°22.4'W; elevation ca. 2000 m. Collected 17 May 1988 by S. J. McKee, W. B. Miller, and R. L. Reeder.

Discussion: Species of *Ashmunella* were reviewed by



Explanation of Figures 1 to 4

Figures 1–3. *Ashmunella milesi* sp. nov. Shell of holotype SBMNH 35609; diameter 13.5 mm. Aperture, apical, and umbilical views respectively. Figure 4. SEM view of typical sculpture (paratype).

PILSBRY (1940) with additional comments provided by BEQUAERT & MILLER (1973) and MILLER (1983). *Ashmunella milesi* is clearly related to the Chiricahuan species of Arizona as indicated by the narrow upper penis shared with those species. It differs from all of those species, however, in that the upper division of the penis is consistently longer. In the specimens dissected, the upper penis is 2.5 times or more the length of the lower portion. No species in the Chiricahuan group has an upper penis greater than 1.5 times that of the lower division.

The shell of *Ashmunella milesi* resembles most closely that of *Ashmunella lenticula* Gregg (see GREGG, 1953). Both species are similar in overall size, the size of the umbilicus, and the sharpness of the shoulder. The parietal tooth is sinuous in *A. lenticula* and relatively straight in *A. milesi*. The extraparietal callous present in many specimens of *A. milesi* is never present in *A. lenticula*.

Distribution and habitat: *Ashmunella milesi* is known only from the type locality, although thorough exploration

of the Sierra Mariquita is incomplete. Vegetation at the type locality consists principally of *Rhus trilobata*, *Yucca shottii*, *Juniperus deppeana*, *Quercus arizonica*, *Quercus oblongifolia*, *Quercus emoryi*, and *Pinus cembroides*.

Etymology: This species is named for Dr. Charles D. Miles, who first introduced me to the study of land snails and sent me off to study them in my beloved desert.

ACKNOWLEDGMENTS

I wish to thank Susan J. McKee for companionship in the field and for preparation of the drawings and photographs. Thanks also to Walt Miller for companionship in the field, the loan of specimens, and reading the manuscript. Jim Hoffman was also kind enough to read the paper. My students Wendy Shaffer and Michael Kalcich helped in the lab, and finally thanks to Dr. Al Soltow and the research office of the University of Tulsa, who kindly financed some of the field work and materials for this study.

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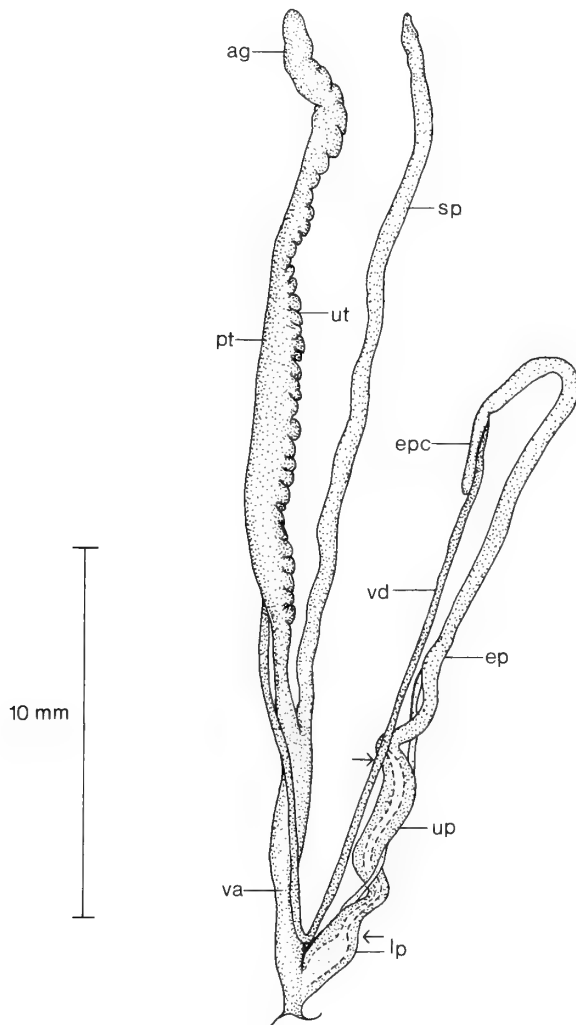


Figure 5

Anterior portion of reproductive system of holotype of *Ashmunella milesi* sp. nov. Drawing prepared from projection of stained wholemount, RLR 813A (SBMNH 35609). Key: ag, albumin gland; ep, epiphallus; epc, epiphallic caecum; lp, lower penis; pt, prostate; sp, spermatheca; up, upper penis; ut, uterus; va, vagina; vd, vas deferens. Arrows indicate limits of upper penis.

First Oligocene Records of *Calyptogena* (Bivalvia: Vesicomidae)

by

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Abstract. Fossils of the vesicomid bivalve *Calyptogena* (*Calyptogena*) *chinookensis* Squires & Goedert, 1991, from probable subduction-related localized limestones in the Lincoln Creek and Pysht formations, and turbidity-flow deposits in middle part of the Makah Formation in western Washington, are the first unequivocal Oligocene records for the genus. Previously, *C. (C.) chinookensis* was known only from late middle to late Eocene subduction-related cold-methane-seep communities in limestones in southwestern Washington. The geologic range of *C. (C.) chinookensis* is now extended from late middle Eocene to late Oligocene. The hinge dentition of this species is observed for the first time and compares well with that of the subgenus *Calyptogena*.

INTRODUCTION

The vesicomid bivalve genus *Calyptogena* includes modern species that can be members of deep-sea chemosynthesis-dependent communities near hydrothermal vents (BOSS & TURNER, 1980), subduction-zone related cold-seeps (OHTA & LAUBIER, 1987), hydrocarbon seeps (KENNICUTT *et al.*, 1985; CALLENDER *et al.*, 1990), and even decaying whale carcasses (SMITH *et al.*, 1989). The fossil record of *Calyptogena* extends from late middle Eocene to Recent (GOEDERT & SQUIRES, 1990; SQUIRES & GOEDERT, 1991). Ancient examples of chemosynthetic communities containing *Calyptogena* are rare and so far have been confined to subduction-related communities in Miocene and Pliocene deposits in Japan (KANNO *et al.*, 1989; NIITSUMA *et al.*, 1989) and late middle to late Eocene limestones in southwestern Washington (GOEDERT & SQUIRES, 1990; SQUIRES & GOEDERT, 1991). These deposits in Washington contain *Calyptogena* (*C.*) *chinookensis* Squires & Goedert, 1991, which is the earliest known species of the genus.

Recent field work indicates that *Calyptogena* (*C.*) *chinookensis* is present sporadically throughout the Paleogene

deep-marine sediments in western Washington State (Figures 1, 2). Newly collected specimens (Figures 3-5) from several Oligocene formations in western Washington allow for a geologic range extension of this species into the late Oligocene and also allow, for the first time, a description of the hinge. Some of the new material is associated with localized limestones that apparently were derived in association with subduction-zone processes. The presence of *C. (C.) chinookensis* in these formations represents the first unequivocal Oligocene occurrences of the genus *Calyptogena*. Previously, BOSS & TURNER (1980:163-164) had tenuously reported *Calyptogena* as ranging from Oligocene to Recent.

The institutional abbreviation, LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, Los Angeles, California, is used for locality and catalog numbers.

MATERIALS AND METHODS

Specimens of *Calyptogena* (*C.*) *chinookensis* were collected from blocks of weathered limestone in the upper part of the Lincoln Creek Formation at locality LACMIP 5843

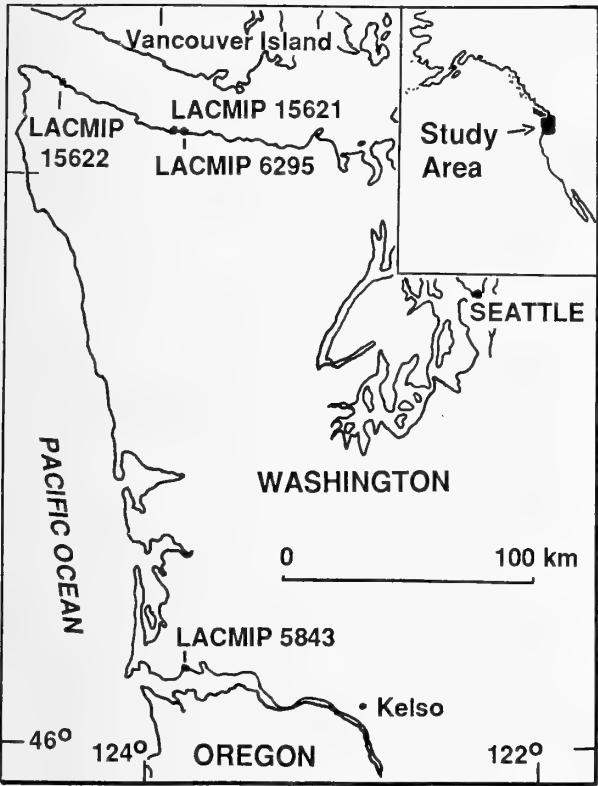


Figure 1

Index map of western Washington State showing new collecting localities for *Calyptogenia* (*C.*) *chinookensis*.

near the townsite of Knappton, Washington (Figure 1). This locality is one of several along the north shore of the Columbia River that have together yielded a diverse and well studied fossil invertebrate fauna (ZULLO, 1982; RIGBY & JENKINS, 1983; MOORE, 1984a, b; SQUIRES, 1989). The presence of *C. (C.) chinookensis* in this fauna was not previously noticed.

At locality LACMIP 5843, most collections of fossils are usually from abundant concretions that have eroded from mudstone exposed on the beach terrace and in modern landslides (MOORE, 1984b). The concretions range in size from a few millimeters to more than 1 m in diameter, and most are barren of fossils. The specimens of *Calyptogenia* (*C.*) *chinookensis* were found in blocks of micritic limestone that have been transported downslope in landslides and are now mixed with the more abundant concretions. The limestone blocks are up to 1 m long and differ from the concretions in being more angular and lighter in color. The limestone blocks also have a strong petroliferous odor when freshly broken, and they contain thin-to-thick wavy crusts of calcite and numerous small tubes or cavities lined with calcite or quartz crystals. The limestone is locally brecciated and usually bioturbated. Where the limestone contains fossils, they are usually articulated specimens of the bivalves *C. (C.) chinookensis* (up to 33 mm length),

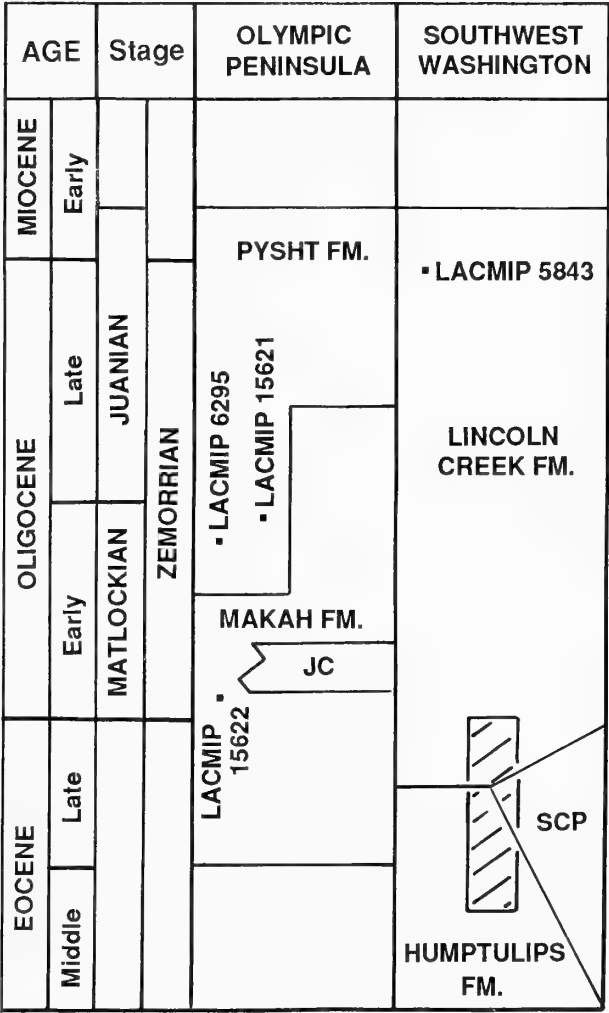


Figure 2

Time-stratigraphic chart showing previous range (slanted lines) of *Calyptogenia* (*C.*) *chinookensis* and position of new localities for this species. Data in part from ARMENTROUT *et al.* (1983). JC = Jansen Creek Member of the Makah Formation; SCP = "Siltstone at Cliff Point" of WELLS (1989).

Thyasira sp. (up to 40 mm length), and *Modiolus willapaensis* Squires & Goedert, 1991 (up to 30 mm length). In addition to these, the limestone also contains rare specimens of the bivalve *Acharax* sp., venerid(?) bivalves, small gastropods, and wood fragments. Some of the thyasirids are hollow and lined with calcite or quartz crystals. A few of the specimens of *Calyptogenia* are partially silicified, and a fragment of the right-valve hinge (Figure 4) was recovered by etching with dilute formic acid.

Specimens of *Calyptogenia* (*C.*) *chinookensis* were also found at localities LACMIP 6295 and LACMIP 15621 in the lower part of the Pysht Formation west of the mouth of Murdock Creek, Clallam County, Washington (Figure 1). Invertebrate macrofossils from these rocks were studied



Explanation of Figures 3 and 4

Figures 3, 4. *Calyptogena (C.) chinookensis* Squires & Goedert, 1991. Figure 3. Left-valve hinge, $\times 6$, hypotype LACMIP 12099, locality LACMIP 15622. Figure 4. Right-valve hinge, $\times 8.9$, hypotype LACMIP 12097, locality LACMIP 5843.

by DURHAM (1944), but he did not note the presence of *Calyptogena*. At these localities, concretions are abundant as lag materials eroded from beach cliffs and the beach terrace along the south shore of the Strait of Juan de Fuca. Mixed with the concretions are blocks of micritic limestone up to 1 m across. This limestone is almost identical to that from the Lincoln Creek Formation at Knappton (LACMIP 5843).

Where the limestone at localities LACMIP 6295 and LACMIP 15621 contain fossils, they are articulated specimens of the bivalves *Calyptogena (C.) chinookensis* (from 5.5 to 25 mm length), *Thyasira* sp. (up to 33 mm length), and *Modiolus willapaensis*? (up to 42 mm length). In addition, the limestone may contain a few pogonophoran(?) tubes, minute gastropods, spatangoid echinoids, crinoid (*Isocrinus*?) parts, and rare wood fragments. Some of the bivalves are hollow and lined with quartz crystals. This limestone has not yet been seen *in situ* at locality LACMIP 6295 or LACMIP 15621, but field observations suggest that the source rock is the same as that producing the abundant concretions.

A few specimens of *Calyptogena (C.) chinookensis* were collected from approximately the middle part of the Makah Formation at locality LACMIP 15622, southeast of the mouth of Bullman Creek, Clallam County, Washington (Figure 1). This locality is in the toe of a modern landslide that largely consists of dark-colored mudstone beds with thin slabs of turbidite sandstone and conglomerate most likely from stratigraphically below the Jansen Creek Member of the Makah Formation. The Jansen Creek Member, which is situated in the middle part of the Makah Formation, is exposed on the beach terrace in all directions from the toe of the landslide. Some of the slabs of thin turbidites eroding from the landslide consist of graded sandstone to pebble conglomerate containing glauconite, foraminifera, some mollusk fragments, rare shark teeth, fish otoliths, and usually articulated specimens of *C. (C.) chinookensis* (22 to 42 mm length) and *Thyasira* sp. (up to 40 mm length). The bivalves are usually together in clusters of several randomly oriented individuals in fine-grained

sediment between larger clasts (up to 9.5 cm across) of siltstone (reworked concretions?) and sandstone. The bivalves do not appear to have been transported, but they have been slightly crushed by sediment compaction. One specimen of *C. (C.) chinookensis* was prepared to reveal the left-valve hinge (Figure 3).

DEPOSITIONAL ENVIRONMENTS AND GEOLOGIC AGES

Molluscan fossils from the upper part of the Lincoln Creek Formation near Knappton, including locality LACMIP 5843, suggest that deposition took place at depths between 100 and 350 m; however, foraminifers indicate a depth of 1000 m or possibly deeper (MOORE, 1984b:7-8). Molluscan fossils referable to the Juanian Molluscan Stage, along with microfossils, indicate a late Oligocene to earliest Miocene age (MOORE, 1984a, b).

Foraminifera from rocks in the vicinity of localities LACMIP 6295 and LACMIP 15621 indicate that deposition probably occurred at a depth of between 300 and 2000 m during late Oligocene (Zemmorian) time (RAU, 1964). Localities LACMIP 6295 and LACMIP 15621 are both within DURHAM's (1944) *Echinophoria rex* Molluscan Zone in the lower part of the "Twin Rivers For-

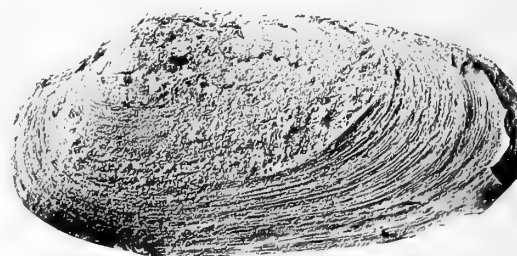


Figure 5

Calyptogena (C.) chinookensis Squires & Goedert, 1991. Left-valve exterior, $\times 3.9$, hypotype LACMIP 12098, locality LACMIP 15621.

mation" (now Pysht Formation of the Twin River Group, see SNAVELY *et al.*, 1977). The *Echinophoria rex* (now *Liracassis rex*) Molluscan Zone is correlative with the Matlockian Molluscan Stage and the lower Zemmorian Foraminiferal Stage, which is early Oligocene in age (MOORE, 1984a). DURHAM (1944) considered these rocks to be middle Oligocene, and DOMNING *et al.* (1986:7) stated that these rocks are middle or late, but not latest, Oligocene in age. The zonal gastropod *Liracassis apta* (Tegland, 1931) has also been collected from this part of the Pysht Formation (GOEDERT, 1988:100). The *L. apta* Molluscan Zone is correlative with the Juanian Molluscan Stage, the upper part of the Zemmorian Foraminiferal Stage, and is late Oligocene to earliest Miocene in age (MOORE, 1984a). The age of the entire Pysht Formation is shown as late Oligocene and earliest Miocene by ARMENTROUT *et al.* (1983). Because both *L. rex* and *L. apta* are present in the lower part of the Pysht Formation west of Murdock Creek, this part of the formation is herein considered temporally equivalent to the upper part of the Makah Formation (Figure 2).

The co-occurrence of *Calyptogena* (*C.*) *chinookensis* in essentially identical limestones at localities LACMIP 5843, LACMIP 6295, and LACMIP 15621, along with the same associations of thyasirid and modiolid species, are much like those previously described from Eocene deep-water strata in western Washington by GOEDERT & SQUIRES (1990) and SQUIRES & GOEDERT (1991). Those Eocene associations were interpreted as fossil cold-methane-seep communities, and the associations from localities LACMIP 5843, LACMIP 6295, and LACMIP 15621 may have also been chemosynthesis-dependent communities supported by cool-fluid seepage.

The occurrence of *Calyptogena* (*C.*) *chinookensis* at locality LACMIP 15622, with associated thyasirids in turbidites of the Makah Formation (Figure 2), is the first in which the species is not in a limestone. *Calyptogena* has been reported living in association with thyasirids in modern turbidity flow deposits (MAYER *et al.*, 1988), and rocks at locality LACMIP 15622 may represent a similar depositional environment. Rocks of the Makah Formation were rapidly deposited in a submarine-fan setting at lower to middle bathyal depths, and are late Eocene to Oligocene in age (SNAVELY *et al.*, 1980). The rocks containing the specimens of *C. (C.) chinookensis* are from below the Jansen Creek Member and are early Oligocene in age. Macrofossils are rare in these deep-water strata, although a few thyasirid, modiolid, and lucinid bivalves have been found associated with fossil cetacean skeletons (SQUIRES *et al.*, 1991). These associations were the first known fossil examples of chemosynthesis-dependent organisms supported by whale bone-oil seepage.

SYSTEMATIC PALEONTOLOGY

Family VESICOMYIDAE Dall & Simpson, 1901

Genus *Calyptogena* Dall, 1891

Type species: *Calyptogena pacifica* Dall, 1891

Subgenus *Calyptogena* s.s.

Calyptogena (*Calyptogena*) *chinookensis*
Squires & Goedert, 1991

(Figures 3–5)

Supplementary description: Right-valve hinge—anterior tooth solid, peglike, and directed posteriorly; central tooth triangular and prolonged anteriorly into a very thin plate that overlaps dorsal part of anterior tooth; posterior tooth area unknown. Left-valve hinge—apparently no anterior tooth; central tooth bifid with a solid posterior part and a thin anterior part; posterior tooth area unknown.

Discussion: The hinge of this species closely resembles that of *Calyptogena* (*C.*) *pacifica* Dall, 1891, illustrated by BERNARD (1974:text fig. 2A) and BOSS & TURNER (1980:fig. 10b). Because of this close similarity, it is herein concluded that *C. chinookensis* should be assigned to the subgenus *Calyptogena*.

BOSS & TURNER (1980) suggested that *Calyptogena* ranged from as early as Oligocene time on the basis of the tenuous inclusion of the genera *Pleurophopsis* Van Winkle, 1919, and *Hubertschenckia* Takeda, 1953, in their synonymy of *Calyptogena*. *Pleurophopsis* is known from Oligocene(?) rocks of the West Indies, Central America, and northwestern South America (KEEN, 1969). The close relationship between *Calyptogena* and *Pleurophopsis unioides* VAN WINKLE (1919:24, pl. 3, fig. 12), the type species of *Pleurophopsis*, was first noted by WOODRING (1938). The geologic age of *P. unioides* remains in question, and it may be as young as Pliocene (BOSS & TURNER, 1980:164).

OLSSON (1931) reported two species of *Pleurophopsis* from probable late Oligocene-age rocks in northern Peru. One of these, *P. lithophagoides* OLSSON (1931:140, pl. 4, figs. 2, 5, 7, 9) shows close affinity with *Calyptogena* (*C.*) *chinookensis*. *Calyptogena* (*C.*) *chinookensis* differs in having the following features: larger size (up to 100 mm length rather than 40 mm), presence of a narrow ridge postero-ventrally from the umbo, and posterior end more tapered.

BOSS & TURNER (1980) mentioned a possible Oligocene occurrence of *Pleurophopsis* from Colombia. The hinge structure is unknown for this specimen(s), and no stratigraphic information was given. As mentioned by OLSSON (1931), *Unio bitumen* COOKE (1919:130, pl. 9, fig. 3a–c) from presumed Oligocene-age rocks in Cuba probably also is congeneric with *Pleurophopsis*. The hinge structure is also unknown for this species, and stratigraphic information is limited.

Hubertschenckia Takeda, 1953, is known from late Oligocene rocks in Japan (TAKEDA, 1953; KEEN, 1969). The close relationship between *Calyptogena* and *Hubertschenckia* was first suggested by KANNO (1971). Future work may prove that these two genera are the same, but *H. ezoensis* (YOKOYAMA, 1890:pl. 25, figs. 6a, b, 7, 8), the type species

of *Hubertschenkia*, has a shell that is much higher relative to length than do most species of *Calyptogena*.

As indicated by BOSS & TURNER (1980), it is quite likely that *Pleurophopsis* and *Hubertschenkia* are actually synonyms for *Calyptogena*. If so, then *Calyptogena* is tenuously known from Oligocene rocks in the West Indies, Central America, northwestern South America, and Japan. The occurrences of *C. (C.) chinookensis* in the upper part of the Lincoln Creek, lower part of the Pysht, and middle part of the Makah formations in Washington are the first unequivocal Oligocene records for this genus and the first report of it in the Oligocene in North America.

ACKNOWLEDGMENTS

We thank Louie Marincovich, Jr. (U.S. Geological Survey, Menlo Park, California) for providing a copy of the hard-to-obtain reference by TAKEDA (1953). Field work that resulted in the discovery of *Calyptogena* in the Pysht and Makah formations was supported by a grant (4439-90) from the National Geographic Society. Gail H. Goedert assisted with field work. We thank Ellen J. Moore and an anonymous reviewer for comments on the manuscript.

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- LACMIP 6295. Float on beach terrace between 300 m and 850 m W of the mouth of Murdock Creek, NW¼ section 29, T31N, R9W, Disque quadrangle (USGS), 7.5 minute, 1950 (photorevised 1978), Clallam County, Washington. Lower part of Pysht Formation. Age: Early(?) Oligocene. Collectors: J. L. & G. H. Goedert, 31 May 1992.
- LACMIP 15621. Limestone blocks on beach terrace, S shore of Strait of Juan de Fuca, approximately 1500 m NW of the mouth of Murdock Creek, 450 m W and 200 m N of the SE corner of section 19, T31N, R9W, Twin Rivers quadrangle (USGS), 7.5 minute, 1950 (photorevised 1979), Clallam County, Washington. Lower part of Pysht Formation. Age: Early(?) Oligocene. Collectors: J. L. & G. H. Goedert, 23 March 1992.
- LACMIP 15622. Thin slabs of turbidite sandstone and pebble conglomerate in dark mudstone in toe of a landslide, approximately 2050 m SE of the mouth of Bullman Creek, NW¼ SW¼ section 22, T33N, R14W, Neah Bay quadrangle (USGS), 7.5 minute,

prov. ed. 1984, Clallam County, Washington. Approximately middle part of Makah Formation (directly below the Jansen Creek Member). Age: Early Oligocene. Collector: J. L. Goedert, 18 May 1992.

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A New *Muricopsis* from the Gulf of California, Mexico

by

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Abstract. A new species of *Muricopsis* collected at Isla Danzante, Gulf of California, Mexico, is described. Originally confused with *Nipponotrophon galapaganus* (Emerson & D'Attilio, 1970), the new species is compared with two closely related congeners, *Muricopsis armatus* (A. Adams, 1854) and *M. jaliscoensis* Radwin & D'Attilio, 1970.

INTRODUCTION

SKOGLUND (1983:108) figured this new species as *Nipponotrophon galapaganus* (Emerson & D'Attilio, 1970) from off Isla Danzante, Gulf of California, Mexico (25°45'N, 111°15'W). VOKES (1988:33) rejected this identification and indicated that the specimen figured by Skoglund was probably a new species of *Muricopsis*. Those identifications were based on a dead specimen lacking protoconch and operculum. In 1989 two living specimens were dredged by Skoglund, and another living specimen was dredged by Hertz and Skoglund in 1991, all at the original location. Our examination of these specimens, including the protoconch, the radula, and the operculum, confirmed that they are not *Nipponotrophon galapaganus* but, indeed, are a new species of *Muricopsis*.

Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York; LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History; and SDNHM, San Diego Museum of Natural History.

SYSTEMATICS

MURICIDAE Rafinesque, 1815

MURICOPSINAE Radwin & D'Attilio, 1971

Muricopsis Bucquoy & Dautzenberg, 1882

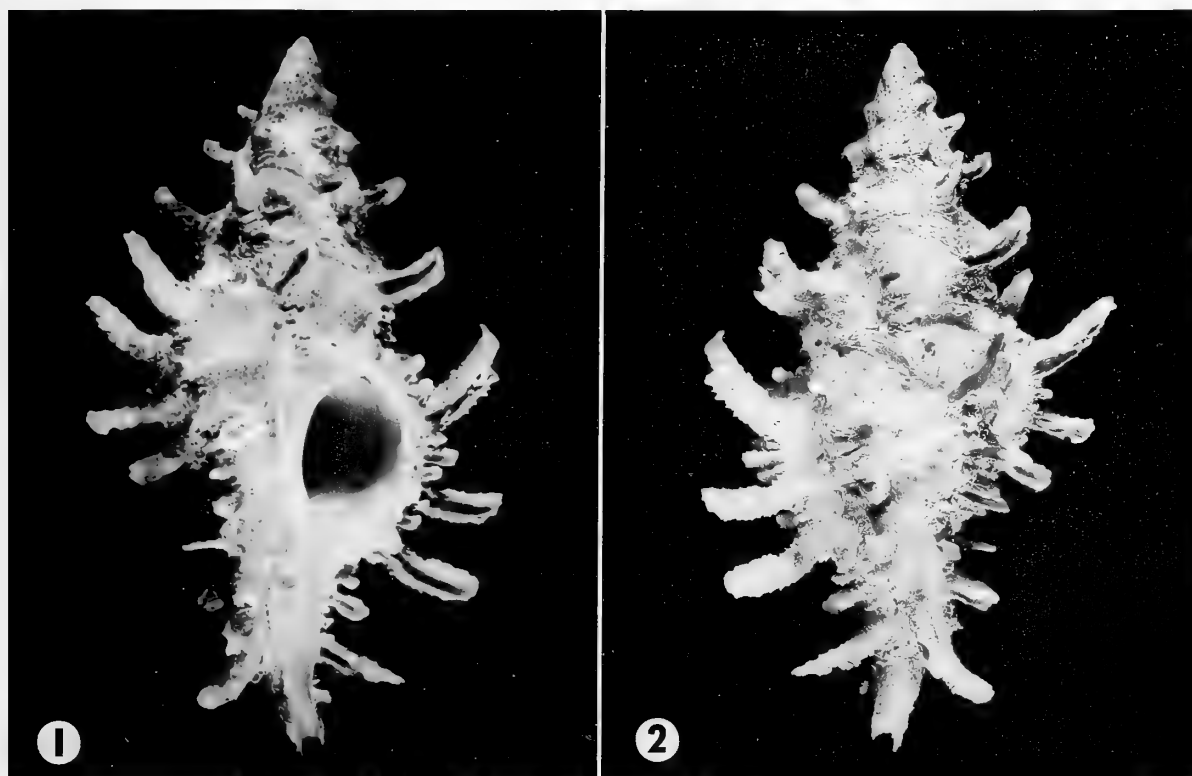
Type species: *Murex blainvillei* Payraudeau, 1826, by original designation

Muricopsis skoglundae

Myers, Hertz & D'Attilio, sp. nov.

(Figures 1–5)

Description: Holotype fusiform; spire high, acute; protoconch eroded (Figures 1, 2). Paratype with a protoconch of 1½ unsculptured, brown, rounded whorls (Figure 3). Suture weakly defined; eight teleoconch whorls; aperture ovate with shallow anal sulcus directed towards columella; outer lip erect, crenulate, reflecting external sculpture, six denticles within, all but most posterior prominent; columellar lip adherent at sulcus, detached and erect below; siphonal canal long, open, recurved. Six varices, crossing shoulder to suture. Four major spiral cords, three on body whorl, one on canal, terminating at each varix in long, recurved, open lamellose spines; minor cords with small lamellose spines between major spines. Canal with gap at juncture of body whorl. Operculum corneous, unguiculate with basal nucleus (Figure 4). Color cream to light tan with single, indistinct brown band on body whorl between second and third major cords. Spines suffused with pale rose; aperture white. Radula with central rachidian tooth and single lateral on each side; rachidian with five cusps, a strong central, two laterals, two minor intermediate cusps, and strong single endpoints (Figure 5).



Explanation of Figures 1 and 2

Figures 1, 2. *Muricopsis skoglundae* sp. nov. Holotype, SBMNH 35610. Height 45.8 mm, width 28.0 mm. Off south end of Isla Danzante, Gulf of California, Mexico, in 30–45 m. Figure 1. Apertural view. Figure 2. Dorsal view.

Etymology: It gives us great pleasure to name the species in honor of Carol Skoglund of Phoenix, Arizona, who collected the first three specimens and has been convinced since 1981 that it was a new species.

Type locality: Just south of Isla Danzante, Gulf of California, Mexico (25°45'N, 111°15'W) in 30–45 m.

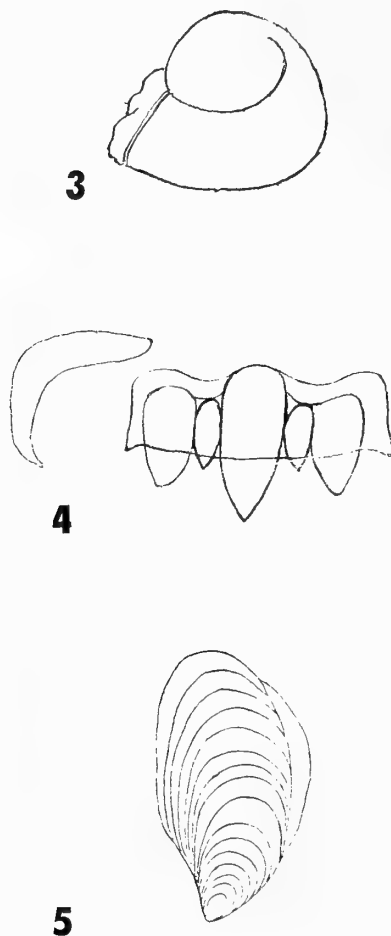
Type material: Three specimens from type locality dredged by Carol and Paul Skoglund, October 1981 and October 1989. Holotype: SBMNH 35610, 45.8 mm long, 28.0 mm wide. Paratypes: AMNH 232521, one specimen 38.3 mm long, 24.8 mm wide; one paratype retained in the Carol Skoglund collection, 26.7 mm long and 21.6 mm wide. One paratype, 48.4 mm long and 27.4 mm wide, dredged by Hertz and Skoglund, October 1991, at type locality, on upper valve of *Hyotissa hyotis* (Linnaeus, 1758), retained in Hertz collection.

Remarks: The AMNH paratype, a dead-collected specimen, is the specimen identified as *Nipponotrophon galapaganus* (Emerson & D'Attilio, 1970) in SKOGLUND (1983). The paratype in the Skoglund collection, a young live-collected specimen with protoconch and immature lip, is tan to light brown with pink spines. The Hertz collection

paratype is a mature, live-collected specimen, with a white to cream shell with a pale rose blush on the long spines.

Discussion: *Muricopsis skoglundae* is compared here with specimens of *M. armatus* in the SDNHM and Skoglund collections, the types of *M. jaliscoensis* (holotype SDNHM 51251; paratypes SDNHM 51250, 51015, 51285) and, for clarity, *Nipponotrophon galapaganus* (holotype AMNH 155906; paratypes AMNH 155907, LACM 1233) and a paratype in the Donald R. Shasky collection.

Muricopsis skoglundae has 1½ unsculptured rounded nuclear whorls. In contrast, *M. armatus*, its closest congener, has 1½ sharply angulate nuclear whorls with shoulder and median cords (MYERS & D'ATTILIO, 1986:71). Although both species have a similar fusiform shape, *M. skoglundae* has only six varices and three major cords on the body whorl, whereas *M. armatus* has seven varices and four major cords on the body whorl. The spines formed where cords and varices intersect are long, recurved and widely open in *M. skoglundae*, compared to *M. armatus*, which has straight, closed or narrowly open spines. There is a prominent knoblike denticle on the columella just above the siphonal canal in *M. armatus*, which is not found in the new species. The prominent gap in spiral sculpture



Explanation of Figures 3 to 5

Figures 3–5. *Muricopsis skoglundae* sp. nov. Figure 3. Paratype, Skoglund collection. Height 26.7 mm, width 21.6 mm. Camera lucida drawing of protoconch. Figure 4. Holotype. Camera lucida drawing of radula. Figure 5. Holotype. Camera lucida drawing of exterior of operculum showing basal nucleus.

between body whorl and canal, and the brown band on the body whorl noted for *M. skoglundae*, are not apparent in *M. armatus*, which has uninterrupted major cords on the body whorl and siphonal canal and no brown band.

Muricopsis skoglundae is quite different from *M. jaliscoensis*, known from Jalisco and Colima in the Gulf of California (RADWIN & D'ATTILIO, 1976) and Panama (D'ATTILIO, 1980:fig. 3 [fig. 1 and 4 should read *M. armatus*]). The shell of *M. skoglundae* is much larger, cream in color, possessing six varices with long spines and few spiral cords, whereas the holotype of *M. jaliscoensis* is brown, half the size of *M. skoglundae*, and has five varices with scabrous spiral cords over the entire surface and short spines. *Muricopsis skoglundae*, with a protoconch of $1\frac{1}{2}$ rounded, unsculptured whorls, has six denticles on the apertural lip and none on the columella, whereas *M. jalis-*

coensis has a two-whorled tabulate protoconch and seven denticles on the apertural lip and three on the columella.

Muricopsis skoglundae has $1\frac{1}{2}$ brown nuclear whorls, whereas *Nipponotrophon galapaganus*, known only from the Islas Galápagos, has $2\frac{1}{2}$ white nuclear whorls. The operculum of *Muricopsis skoglundae* has a basal nucleus, whereas in *Nipponotrophon galapaganus* the nucleus is situated sublaterally (EMERSON & D'ATTILIO, 1970:fig. 4). *Muricopsis skoglundae* has scabrous sculpture and no intritacalx. In contrast, *Nipponotrophon galapaganus* has a smooth shell covered by a thick white intritacalx. The shell of *Muricopsis skoglundae* has strong varical spines which continue on the siphonal canal; *Nipponotrophon galapaganus* has no spines on the siphonal canal.

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We are grateful to William K. Emerson of the American Museum of Natural History, James H. McLean and Lindsey Groves of the Natural History Museum of Los Angeles County, and Donald R. Shasky of Redlands, California, for the loan of type material. The San Diego Natural History Museum made its facilities available to us and Regina Wetzter, Collections Manager, Department of Marine Invertebrates, kindly assisted in the mounting of the minute radula of *Muricopsis skoglundae*. We are indebted to David K. Mulliner, who photographed the holotype of the new species. William K. Emerson, James H. McLean, Walter E. Sage III, and Emily H. Vokes kindly reviewed the manuscript. Finally, Carol Skoglund is especially thanked for giving us the opportunity to describe this beautiful new species.

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First Report of the Ovulid Gastropod
Sulcocypraea mathewsonii (Gabb, 1869) from the
Eocene of Washington and Oregon and an
Additional Report from California

by

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Abstract. The warm-water ovulid gastropod *Sulcocypraea mathewsonii* (Gabb, 1869), previously known only from middle Eocene strata in southern and central California, is reported for the first time from middle Eocene strata in western Washington, as well as from an additional locality in southern California. The species is tentatively reported from middle Eocene strata in northwestern and southwestern Oregon. The Washington locality is the northernmost record of any ovulid, fossil or living, in the eastern Pacific, and extends the geographic range of this species northward 1100 km. The geologic range of *Sulcocypraea* is restricted to the earliest Eocene to early Oligocene.

INTRODUCTION

Sulcocypraea (family Ovulidae) is an uncommon Paleogene gastropod genus known only from seven species in North America, one species in northern Peru, and one species in southwestern France. We report here new geographic records for the genus from middle Eocene strata in western Washington and southern California, and tentatively from middle Eocene strata in northwestern and southwestern Oregon. The Washington record, from a locality just south of Seattle (47°30'N latitude) is the northernmost for any ovulid, fossil or living, in the eastern Pacific.

Ovulid gastropods live today in tropical to subtropical seas (ROSENBERG, 1992), and the presence of *Sulcocypraea* in Washington and Oregon indicates similar conditions. This would be in keeping with what has been reported for the paleoclimate of this area during the middle Eocene. On the basis of reef-coral genera and numerous genera of mollusks whose species today are particularly characteristic of warm waters, DURHAM (1950, 1952, 1959) re-

ported that the tropics extended somewhat northward of 49°N latitude along the Pacific coast of North America during most of the Eocene.

Abbreviations used for catalog and/or locality numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences, San Francisco; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California Museum of Paleontology (Berkeley); UCR, University of California, Riverside; UWBM, University of Washington (Seattle), Thomas Burke Memorial Washington State Museum (= UW in older literature).

NEW STRATIGRAPHIC DISTRIBUTION

The new stratigraphic report in Washington is from the Tukwila Formation just south of Seattle (Figure 1). Intensive collecting during a seven-year period (1981–1988) by personnel of UWBM yielded 11 specimens of *Sulcocypraea mathewsonii* (Gabb, 1869). Ten of these specimens

are from UWBM loc. A7561, informally known as the Poverty Hill site. They supplement a single specimen collected by C. E. Weaver from UWBM loc. 11, essentially equivalent to UWBM loc. A7561. Weaver's specimen is deposited also at UWBM. A twelfth specimen is from UWBM loc. 229 in the immediate vicinity of UWBM loc. A7561. The specimens are internal molds for the most part, but eight of them do retain some remnants of shell material.

Sedimentary rocks in the Poverty Hill area south of Seattle have been mapped as the Tukwila [*sic*] Formation by McWILLIAMS (1971). Fossils in this area are found in current-concentrated shell beds that are interstratified with poorly sorted, barren basaltic sandstone layers. McWilliams listed 39 species of shallow-water subtropical mollusks from these shell beds, but he did not include *Sulcocypraea matthewsonii*. ARMENTROUT *et al.* (1983) correlated the Tukwila Formation to the middle and upper Eocene and assigned most of the formation to the Bartonian Stage (upper middle Eocene), approximately coeval with the Cowlitz Formation in southwestern Washington.

The 12 specimens from the Tukwila Formation near Seattle extend the geographic range of this species northward about 1100 km. Previously, this species was known only as far north as near Martinez, Suisun Bay, Contra Costa County, north-central California.

Specimens only tentatively identified as *Sulcocypraea matthewsonii* are recognizable in collections from both northwestern and southwestern Oregon. A single specimen from the Hamlet formation (informal name of NIEM & NIEM, 1985) near Portland in northwestern Oregon (Figure 1) is poorly preserved and only identified as *S. cf. S. matthewsonii*. The internal mold was collected by Gregory J. Rettack in an area known as the Rocky Point quarry locality (LACMIP loc. 15649). The fossils are in bouldery rubble derived from basaltic headlands and deposited in pocket beaches along a storm-dominated rocky coastline (MUMFORD & NIEM, 1992). Previous workers (WARREN & NORBISRATH, 1946; STEERE, 1957; NIEM & VAN ATTA, 1973:90) listed as many as 18 species of marine invertebrates from the vicinity of this locality, but no mention was made of *S. matthewsonii*. The strata at this locality were formerly regarded by these previous workers as part of the Cowlitz or Goble formations, but MUMFORD & NIEM (1992) correlated the fossiliferous basaltic conglomerate to the basal Roy Creek member of the Hamlet formation. They reported abundant calcareous nannofossils indicative of the CP14a and CP14b Zones from the upper part of the Hamlet formation. AUBREY *et al.* (1988) assigned these zones to the late middle Eocene. The age of the *Sulcocypraea* specimen, which is from beds lower in the Hamlet formation, is herein regarded as approximately late middle Eocene in age.

Another single, poorly preserved specimen tentatively identified as *Sulcocypraea cf. S. matthewsonii* is from the Tyee Formation in southwestern Oregon (Figure 1). This locality, informally known as the Comstock overpass lo-



Figure 1

Index map of new and previous localities of *Sulcocypraea matthewsonii* (Gabb, 1869).

cality (UCMP loc. A-1134), was first mentioned by DILLER (1896:460). TURNER (1938:19) recorded an invertebrate fauna of more than 20 species from this locality and identified one of the species as *Cypraea* sp. B. It is based on a single specimen of *Sulcocypraea cf. S. matthewsonii* that consists of an internal mold with only a small remnant of



Explanation of Figures 2 to 4

Figures 2–4. *Sulcocypraea mathewsonii* (Gabb, 1869), hypotype UWBM 22052 from UWBM loc. A7561, internal mold, $\times 3.3$. Figure 2: apertural view. Figure 3: abapertural view. Figure 4: right lateral view.

shell in the posterior outer lip area. HOOVER (1963), who did detailed geologic mapping in the area, gave an updated version of Turner's check list from UCMP loc. A-1134 and mentioned *Cypraea* sp. B of Turner. The locality was shown by HOOVER (1963) to be in the Tyee Formation. He also listed a microfossil assemblage from this locality and mentioned that the microfauna is similar to that of the Elkton siltstone member of the Tyee Formation in the lower Umpqua River area, Oregon. Recent workers (HELLER & DICKINSON, 1985; MOLENAAR, 1985) interpreted the depositional setting of the stratigraphically complex Tyee Formation to be a delta-fed submarine fan and assigned the formation to the middle Eocene.

A new record of *Sulcocypraea mathewsonii* in southern California was detected in the UCR invertebrate paleontology collection. It is a single specimen from UCR loc. 4750 in the upper half of the Juncal Formation in the Pine Mountain area, Ventura County, southern California. The specimen was collected from a lens of conglomeratic sandstone by GIVENS (1974) but not mentioned by him in his study of the fauna. The locality, situated at the boundary between sandstone (inner sublittoral) and siltstone (inner sublittoral to deltaic complex), was assigned by GIVENS (1974:table 1) to the *Turritella uvasana applinae* faunal zone, or approximately the middle Eocene ("Domengine Stage").

SYSTEMATIC PALEONTOLOGY

Family OVULIDAE Fleming, 1828

Subfamily EOCCYPRAEINAE Schilder, 1924

Genus *Sulcocypraea* Conrad, 1865

Type species: *Cypraea lintea* Conrad, 1847 [1848], by monotypy, lower Oligocene (Rupelian Stage), Byram Formation, Vicksburg Group, Mississippi.

Remarks: Because SCHILDER (1924, 1927) and SCHILDER & SCHILDER (1971) assigned *Sulcocypraea* to the subfamily Eocypraeinae, family Amphiperatidae (= Ovulidae) we have provisionally followed their classifications. However, the morphology of most fossil genera of Eocypraeinae suggest that they belong within the family Cypraeidae, a concept that is beyond the scope of this paper.

Sulcocypraea mathewsonii (Gabb, 1869)

(Figures 2–4)

Cypraea (*Epona*) *mathewsonii* GABB, 1869:164, 225, pl. 27, figs. 44a, b; ARNOLD, 1906:15; KEEN & BENTSON, 1944:152.

Cypraea mathewsonii Gabb, 1869: WHITEAVES, 1895:128; DICKERSON, 1916:421, 438, 448; ANDERSON & HANNA, 1925:43, 107; NELSON, 1925:425; STEWART, 1926 [1927]:371, pl. 28, fig. 5; INGRAM, 1942:105, pl. 2, figs. 10–11; INGRAM, 1947a:61; INGRAM, 1947b:147; WEAVER, 1953:43; RICHARDS, 1968:156. [*Non* DICKERSON, 1915:43, 60, pl. 6, fig. 5a.]

Cypraea kerniana ANDERSON & HANNA, 1925:43, 104–105, 107, pl. 13, figs. 9–11; CLARK, 1926:115; HANNA, 1927:314, pl. 52, figs. 7, 9; STEWART, 1926 [1927]:371; KEEN & BENTSON, 1944:152.

Sulcocypraea mathewsonii (Gabb, 1869): SCHILDER, 1927:81; SCHILDER, 1941:104.

Sulcocypraea mathewsonii mathewsonii (Gabb, 1869): SCHILDER, 1932:222; SCHILDER & SCHILDER, 1971:68, 131.

Sulcocypraea kerniana (Anderson & Hanna, 1925): SCHILDER, 1932:222; SCHILDER, 1941:104; SCHILDER & SCHILDER, 1971:68, 125; DOLIN & DOLIN, 1983:44.

Cypraea sp. B: TURNER, 1938:19, 35; HOOVER, 1963:27.

Luponovula mathewsonii (Gabb, 1869): DOLIN & DOLIN, 1983:42–45, figs. 28, 29a–c.

Type material and type locality: Of *Cypraea mathewsonii*, holotype, ANSP 4217; Eocene "Tejon Group" near Martinez, Contra Costa County, California (GABB, 1869). Of *C. kerniana*, holotype, CAS 245.02 (*ex* CAS 816) and paratypes, CAS 245.03 and 245.04 (*ex* CAS 817, 818); Grapevine Creek, Kern County, California (CAS loc. 245), Eocene "Type" Tejon Formation (ANDERSON & HANNA, 1925).

Geographic distribution: Seattle, King County, Washington to San Diego, San Diego County, southern California.

Stratigraphic distribution: California "Domengine Stage"

(middle Eocene part) to "Tejon Stage," equivalent to middle to upper middle Eocene (Lutetian to Bartonian Stages) (see SQUIRES, 1988). "DOMENGINE STAGE": Tentatively the Tyee Formation, southwestern Oregon (TURNER, 1938; HOOVER, 1963); Muir Sandstone, near Martinez, Contra Costa County, north-central California (WEAVER, 1953); upper Juncal Formation, Pine Mountain area, southern California (herein); Rose Canyon Shale Member, La Jolla Formation [= Ardath Shale] (DICKERSON, 1916; CLARK, 1926; HANNA, 1927). "TEJON STAGE": Tukwila Formation, Seattle, Washington (herein); tentatively the Hamlet formation (informal), northwestern Oregon (herein). "DOMENGINE STAGE"/"TEJON STAGE" UNDIFFERENTIATED: "Tejon Group," Eocene, near Martinez, Contra Costa County, north-central California (GABB, 1869; ARNOLD, 1906; STEWART, 1926 [1927]; SCHILDER, 1932; INGRAM, 1942; RICHARDS, 1968); "Type" Tejon Formation, Grapevine Canyon area, south-central California (GABB, 1869; DICKERSON, 1915; DICKERSON, 1916; ANDERSON & HANNA, 1925; CLARK, 1926).

Remarks: Because of morphologic similarities, *Sulcocypraea kerniana* was judged by SCHILDER & SCHILDER (1971) to be a primary junior synonym of *S. mathewsonii*.

The only other species of *Sulcocypraea* known from the Pacific coast of North America is *Cypraea oakvillensis* Van Winkle, 1918, based on a single specimen from UWBM loc. 169 in the Eocene-Oligocene Lincoln Creek Formation, near Oakville, Grays Harbor County, western Washington, approximately 105 km southwest of Seattle. VAN WINKLE (1918) assigned *C. oakvillensis* to the *Barbatia merriami* zone, which ARMENTROUT (1975: fig. 2) correlated with the uppermost Eocene *Echinophoria dalli* zone of the Pacific Northwest Galvinian Stage. *Sulcocypraea oakvillensis* was treated as a subspecies of *S. mathewsonii* by SCHILDER & SCHILDER (1971), but the holotype (CAS 61715.01 [ex UWBM 140]) of *S. oakvillensis* was too poorly preserved to justify this assignment. The holotype of *S. oakvillensis* is now missing, and the available illustrations (VAN WINKLE, 1918: pl. 7, fig. 19; INGRAM, 1942: pl. 2, figs. 14–15; 1947a: pl. 2, figs. 15–16; WEAVER, 1942 [1943]: pl. 76, figs. 29–30) are unsatisfactory because of the poor preservation. Until additional topotypes of *S. oakvillensis* are found, which seems unlikely due to poor exposures in the area (W. C. Wehr, personal communication), the name should be treated as a *nomen dubium*.

Five species of *Sulcocypraea* are known from the Gulf coast of North America. *Sulcocypraea perinflata* (Schilder, 1927), from Alabama, is the earliest species of the genus. HARRIS (1896) reported this species from "upper Lignitic" strata at Woods Bluff on the Tombigbee River, Clarke County, Alabama, but he mistakenly referred to the species as *Cypraea smithii* Aldrich, 1886. TOULMIN (1977) placed the Woods Bluff locality in the lower Eocene Bashi Marl Member of the Hatchebigee Formation, and DOCKERY (1986) assigned the Bashi Marl Member to the lowermost

Eocene. Other described species are *Sulcocypraea kennedyi* (Harris, 1895) from the middle Eocene of Mississippi, Texas, and South Carolina; *S. vaughani* (Johnson, 1899) from the upper Eocene of Mississippi, Louisiana, and South Carolina (PALMER & BRANN, 1966; DOCKERY, 1980); and *S. lintea* (Conrad, 1847 [1848]) and *S. healeyi* (Aldrich, 1923) [= *S. dalli* (Aldrich, 1894), preoccupied] from the lower Oligocene of Mississippi and Mississippi and Louisiana, respectively (MACNEIL & DOCKERY, 1984).

The only South American species of *Sulcocypraea* is *Amphiperas bullenewtoni* Olsson, 1930, from the middle Eocene Talara Formation, at Yasila, Piura Dept., Peru (BRANN & KENT, 1960). The only species of *Sulcocypraea* known from anywhere else in the world is one morphologically close to *S. mathewsonii* from Eocene rocks near Pau, Pyrenees-Atlantiques, in the Béarn Basin of southwestern France (DOLIN & DOLIN, 1983).

A review by Groves (in preparation) of *Sulcocypraea* suggests that all of the northeastern Pacific species of this genus and the southwestern France species may belong to a new subgenus of *Sulcocypraea*. Species from the Gulf coast and Peru appear to belong to *Sulcocypraea*, *sensu stricto*.

The geologic range of *Sulcocypraea* was previously reported to be middle Paleocene to late Oligocene (WENZ, 1941; SCHILDER & SCHILDER, 1971) but is refined herein to range from the earliest Eocene to early Oligocene.

ACKNOWLEDGMENTS

We thank James L. Goedert (Gig Harbor, Washington) for informing us about the Tukwila Formation ovoid specimens and for information about the Rocky Point locality. Wesley C. Wehr (UWBM) kindly located all the Poverty Hill specimens and enthusiastically supplied much information about the associated molluscan fauna. He and V. S. Mallory (UWBM) provided casts of the holotype of *Sulcocypraea oakvillensis*. Ronald C. Eng (UWBM) efficiently provided for the loan of the specimens.

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George L. Kennedy (LACMIP), James H. McLean (Natural History Museum of Los Angeles County, Malacology Section), and two anonymous reviewers critically read the manuscript.

LOCALITIES CITED

- CAS loc. 245. Along the east bank of a small gulch about 0.4 km E of the pumping plant located near the mouth of Grapevine Creek, Kern County, California (ANDERSON & HANNA, 1925:39). "Type" Tejon Formation (in the broad sense). Age: Middle to possibly late middle Eocene. Collector: B. G. Martin.
- LACMIP loc. 15649. Rocky Point quarry, also known as the Columbia County quarry, (= Stop 5 of STEERE, 1957:40, and Stop 1-3 of NIEM *et al.*, 1973:99-100, fig. 3), at end of access road 0.2 km W of Timber-Vernonia road 10.5 km SW of Vernonia or 9.4 km N of junction on State Highway 26 and Timber-Vernonia road, in E central part of section 22, T4N, R5W, U.S. Geological Survey, 7.5-minute, Clear Creek, Oregon, quadrangle, 1979, Columbia County, northwestern Oregon. Basalt is exposed at base of abandoned quarry, but overlying the basalt is about 5 m of basal conglomerate containing many marine fossils. Locality approximately same as LACMIP loc. 5887. Basal Roy Creek member of the Hamlet formation (informal names). Age: Late middle Eocene. Collector: G. J. Retallack.
- UCMP loc. A-1134. Comstock overpass locality (= locality M-12 of HOOVER, 1963:26, pl. 1), in road-cut at E end of old Pacific Highway overpass at old railroad siding 0.8 km S of Comstock (TURNER:1938, fig. 5), NE¼ section 20, T21S, R4W, U.S. Geological Survey, 7.5-minute, Curtin, Oregon, quadrangle, provisional edition 1987, Douglas County, southwestern Oregon. Tyee Formation. Age: Middle Eocene. Collector: F. E. Turner, 1938.
- UCR loc. 4750. On crest of ridge 823 m (2700 ft) W of elevation 6200 on San Guillermo Mountain (see GIVENS, 1974:100 and geologic map), 152 m (500 ft) N, 213 m (700 ft) W of SE corner of section 13, T7N, R22W, U.S. Geological Survey, 7.5-minute, San Guillermo, California, quadrangle, 1943, Ventura County, southern California. Age: Middle Eocene. Collector: C. R. Givens, 1974.
- UWBM loc. 11. In sandstone at NE corner of rock outlier at Duwamish station, section 10, T24N, R4E, U.S. Geological Survey, 7.5-minute, Seattle South, Washington, quadrangle, 1949 (photorevised 1968 and 1973), King County, western Washington. Same as UWBM loc. A7561. Tukwila Formation. Age: Late middle Eocene. Collector: C. E. Weaver, 1909.
- UWBM loc. 169. Oakville quarry, in sandstone overlying basalt, 1.6 km W of Oakville, on Burlington Northern railroad track, section 19, T16N, R4W, U.S. Geological Survey, 15-minute, Rochester, Washington, quadrangle, 1953, Grays Harbor County, western Washington. Lincoln Creek Formation. Age: Latest Eocene. Collector: K. E. H. Van Winkle, 1918.
- UWBM loc. 229. Approximately 600 m N22°E from UWBM loc. A7561 (see below) in section 3, T23N, R4E, (see McWILLIAMS, 1971:fig. 1), N side of Duwamish River area, S of Seattle, King County, Washington, U.S. Geological Survey, 7.5-minute, Seattle South, Washington, quadrangle, 1949 (photorevised 1968 and 1973), King County, western Washington. Tukwila Formation. Age: Late middle Eocene. Collector: V. S. Mallory.
- UWBM loc. A7561. Poverty Hill, S of Boeing Field, where NE corner of the hill in section 10 intersects the section boundary between sections 3 and 10 in T23N, R4E, N side of Duwamish River area, approximately 0.4 km W of intersection of Interstate Highway 5 and Martin Luther King Way (formerly Empire Way), U.S. Geological Survey, 7.5-minute, Seattle South, Washington, quadrangle, 1949 (photorevised 1968 and 1973), King County, western Washington. Same as UWBM loc. 11. Tukwila Formation. Age: Late middle Eocene. Collectors: C. E. Weaver, 1909; Eric Brown, Terrence Frest, Edward Johannes, V. S. Mallory, Mark Reeves, N. Smith, Ted Weasma, and W. C. Wehr, 1981-1988.

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New Records for Ranellid Gastropods in the Western Atlantic (Ranellidae: Cymatiinae)

by

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Abstract. Additional confirmation is given for the presence of *Cymatium* (*Monoplex*) *mundum* (Gould, 1849) in the western Atlantic. *Cymatium* (*Turritriton*) *vespaceum* (Lamarck, 1822) is authenticated from Florida and Honduras; *Cymatium* (*Reticutriton*) *pfeifferianum* (Reeve, 1844) is reported for the first time from Florida and Brazil; and *Cymatium* (*Ranularia*) *gallinago* (Reeve, 1844) is reported from Brazil.

INTRODUCTION

Although several prosobranch gastropod families have species with teleplanic larvae, such species are especially common in Ranellidae. Some of these larvae are very long-lived and this enables them to disperse over a large area. During recent examinations of private and museum collections and a collecting trip to Brazil, I found specimens that confirmed and extended the ranges of the species cited herein.

Collections studied are as follows: AMNH—American Museum of Natural History, New York, New York; DMNH—Delaware Museum of Natural History, Wilmington, Delaware; García Coll.—Dr. E. F. García, Lafayette, Louisiana; NHM(L)—The Natural History Museum,

London (formerly the British Museum [Natural History]); Piech Coll.—B. J. Piech, Wilmington, Delaware; Sunderland Coll.—Kevan and Linda Sunderland, Sunrise, Florida; Trinchão Coll.—Luiz Trinchão, Salvador, Bahia, Brazil; Voss Coll.—Carolyn Voss, Hammond, Louisiana.

WESTERN ATLANTIC RECORDS OF FOUR SPECIES OF RANELLIDAE

Cymatium (*Monoplex*) *mundum* (Gould, 1849)

(Figures 1, 2)

In the past, *Cymatium mundum* was usually placed in synonymy with *Cymatium* (*Monoplex*) *gemmatum* (Reeve,

Explanation of Figures 1 to 16

Figures 1-16. *Cymatium*. Photography by the author.

Figure 1. *Cymatium mundum*; Sunderland Coll.; Key West, Florida; 38 mm.

Figure 2. *C. mundum*; Sunderland Coll.; Key West, Florida; 29 mm.

Figure 3. *C. vespaceum*; Piech Coll.; Roatan, Honduras; 41 mm.

Figure 4. Dorsal view of Figure 3.

Figure 5. *C. vespaceum*; Sunderland Coll.; Key Largo, Florida; 22 mm.

Figure 6. Dorsal view of Figure 5.

Figure 7. *C. pfeifferianum*; Voss Coll.; Todos Santos Bay, Bahia, Brazil; 46 mm.

Figure 8. Dorsal view of Figure 7.

Figure 9. *C. pfeifferianum*; Piech Coll.; Australia; 60 mm.

Figure 10. Dorsal view of Figure 9.

Figure 11. *C. gallinago*; figured syntype, NHM(L), No. 1967593; 61 mm.

Figure 12. Dorsal view of Figure 11.

→

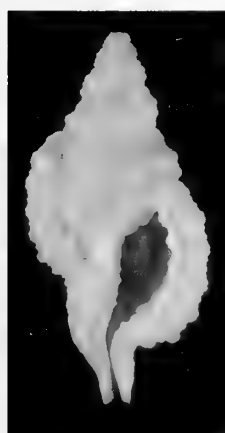


Figure 1

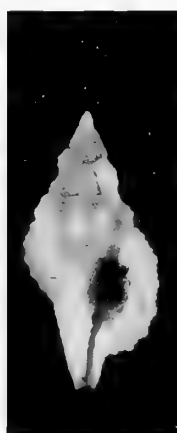


Figure 2



Figure 3



Figure 4



Figure 5

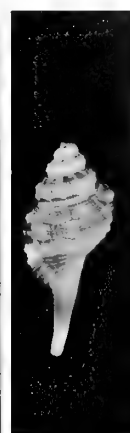


Figure 6

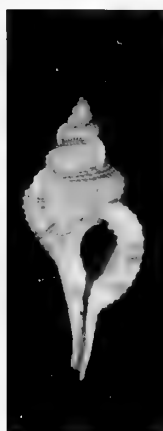


Figure 7

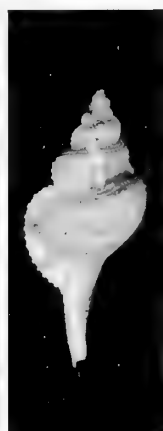


Figure 8

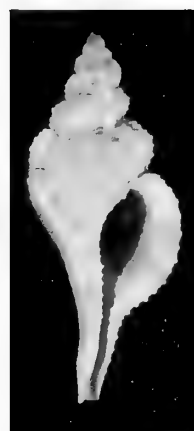


Figure 9

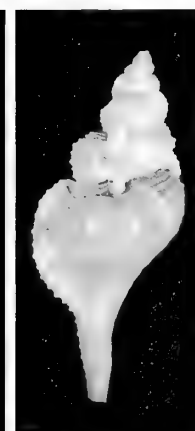


Figure 10

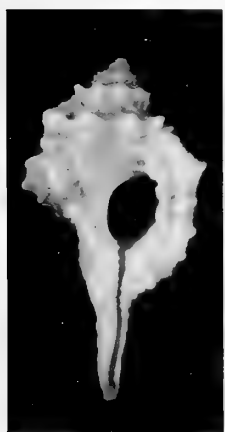


Figure 11

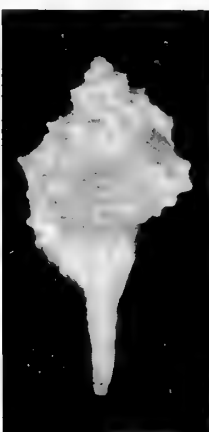


Figure 12

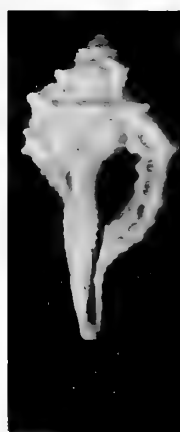


Figure 13

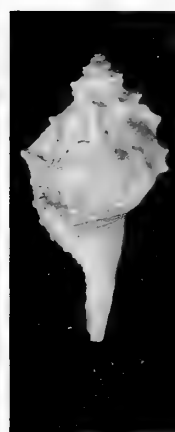


Figure 14

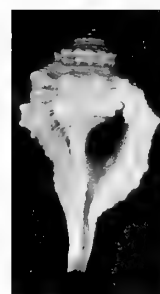


Figure 15

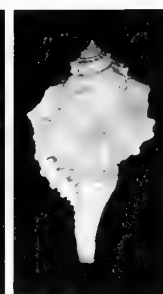


Figure 16

Figure 13. *C. gallinago*; Piech Coll.; Todos Santos Bay, Bahía, Brazil; 61 mm.

Figure 14. Dorsal view of Figure 13.

Figure 15. *C. gallinago*, Piech Coll.; Madagascar; 49 mm.

Figure 16. Dorsal view of Figure 15.

1844). Then BEU (1985:58) listed both species as valid and this was later confirmed by EMERSON (1991:63). *Cymatium mundum* is very common in the Indo-Pacific but only two specimens have been previously recorded from the western Atlantic (EMERSON, 1991:65). Here two additional records (3 specimens) from that area are reported.

- (1) AMNH: No. 181298, 1 specimen; Frank Lyman Family, 1940 (as "*Cymatium vespacum*," originally labeled as "*Cymatium gracilis*, extremely rare," dredged 149 m, off Palm Beach County, Florida; 25 mm.
- (2) Sunderland Coll.: 2 specimens; from shrimp boats, 1978; 185 m, off Key West, south of the Dry Tortugas, Florida; 29 mm (with operculum) and 38 mm.

It has been suggested that *C. mundum* might be only a shallow-water form of a deep-water *C. gemmatum*. These deep-water specimens of *C. mundum*, taken in 149 m and 185 m, refute that idea.

Cymatium (Turritriton) vespacum
(Lamarck, 1822)

(Figures 3–6)

Until recently, *Cymatium vespacum* was considered a valid species in most of the tropical areas of the world including the western Atlantic. ABBOTT (1974:163, fig. 1754 [sic; = 1755]) showed a specimen from that area (Matanzas, Cuba), copying the figure cited by CLENCH & TURNER (1957:223, pl. 125, fig. 1) as *C. gemmatum*. Actually those figures appear to show what is now called *Cymatium (Turritriton) comptum* (A. Adams, 1854) since BEU (1985:60) has separated *C. comptum* from *C. vespacum*, placing the former in the Indo-Pacific and eastern and western Atlantic, and restricting *C. vespacum* to the Indo-Pacific.

My subsequent examination of numerous specimens labeled as *Cymatium vespacum* from the western Atlantic confirmed that most of them should be referred to *C. comptum*. However, two specimens of *C. vespacum* from that area have been verified, so the western Atlantic must be included in its range.

- (1) Piech Coll.: 1 specimen; self-collected, crabbed, May 1980; Roatan Island, Honduras; 41 mm.
- (2) Sunderland Coll.: 1 specimen (juvenile); self-collected, dead, 1978; 4.5 m, Pickle's Reef off Key Largo, Florida; 22 mm.

Cymatium (Reticutriton) pfeifferianum (Reeve, 1844)

(Figures 7–10)

This *Cymatium* species previously had been reported only from the Indo-West Pacific (BEU, 1985:59). As a result of my recent examination of the five western Atlantic specimens listed below, the range of *C. pfeifferianum* should now include that area.

- (1) DMNH: No. 74116, 2 very juvenile but identifiable specimens; ex J. W. Poling, 16 February 1971; 46 m, W of Egmont Key, Florida; 10 mm and 28 mm.

- (2) Trinchão Coll.: 2 specimens, not measured; self-collected, dead, no date; Todos Santos Bay, Bahía, Brazil.
- (3) Voss Coll.: 1 specimen; self-collected, dead, 1979–1980; beachwash, Todos Santos Bay, Bahía, Brazil; 46 mm.

As additional confirmation, I recently had the opportunity to talk with Professor Eliézer de C. Rios (1992) and see the manuscript of his up-coming book *Seashells of Brasil*, 2nd ed. The following is an excerpt from page 121: "*Cymatium pfeifferianum* (Reeve, 1844) Australia to Japan, Philippines Is.—Northeast Brasil. . . . Only Brazilian record: Itaparica Is., Bahía, from hermit-crabs (B. Linhares)."

Cymatium (Ranularia) gallinago (Reeve, 1844)

(Figures 11–16)

REEVE (1844:pl. II, sp. 5) and BEU (1985:59) list *Cymatium gallinago* as a western Pacific species, although all the specimens that I have examined previously have been from the Indian Ocean. Seven specimens from Brazil are reported here and that country must now be included in its range.

These seven specimens, listed below, were misidentified as *Cymatium (Ranularia) trilineatum* (Reeve, 1844). After comparison with Reeve's syntypes of these two species that were borrowed from NHM(L) (*C. trilineatum* No. 1967627 and *C. gallinago* No. 1967593), all seven specimens are definitely referable to *C. gallinago*.

- (1) García Coll.: 1 specimen; self-collected, dead, August 1991; beachwash, Itaparica Island, Todos Santos Bay, Bahía, Brazil; 62 mm, siphonal canal broken.
- (2) Piech Coll.: 1 specimen; collected by Luiz Trinchão, dead, no date; Todos Santos Bay, Bahía, Brazil; 61 mm.
- (3) Piech Coll.: 1 specimen; self-collected, dead, August 1991; beachwash, Itaparica Island, Todos Santos Bay, Bahía, Brazil; 34 mm, siphonal canal broken.
- (4) Trinchão Coll.: 2 specimens; self-collected, dead, no date; Todos Santos Bay, Bahía, Brazil; not measured.
- (5) Voss Coll.: 2 specimens; self-collected, dead, 1979–1980; beachwash, Todos Santos Bay, Bahía, Brazil; 53 mm and 54 mm, larger one with broken siphonal canal.

ACKNOWLEDGMENTS

I would like to express my appreciation to Dr. E. F. García, Kevan and Linda Sunderland, and Carolyn Voss for furnishing specimens for study; to Kathie Way, NHM(L), for loaning syntypes; and to Mary Jane Arden, DMNH, for her assistance with graphics. Dr. A. G. Beu, DSIR Geology and Geophysics, Lower Hutt, New Zealand, and Dr. William Emerson and Walter Sage III, AMNH, reviewed my manuscript and offered many helpful suggestions. I thank them and the other reviewers for their constructive comments. A special note of credit and appreciation

must go to Luiz Trinchão of Salvador, Bahía, Brazil, for calling to my attention the occurrence of *Cymatium pfeifferianum* and *C. gallinago* in his country.

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NOTES, INFORMATION & NEWS

**Predation by *Latiaxis oldroydi*
(Gastropoda: Coralliophilidae) on
Corynactis californica
(Anthozoa: Corallimorphidae)**

by

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The subtidal gastropod *Latiaxis oldroydi* (I. Oldroyd, 1929) ranges from Point Conception, California, to Cedros Island, Baja California, Mexico (McLEAN, 1978). ROBERTSON (1970) reported that species of the family Coralliophilidae usually are suctorial predators on stony corals, although a few species also were reported to feed on gorgonians, zoanthids, antipatharians, and alcyonarians.

On 15 December 1990, one of us (MKW) collected two specimens of *Latiaxis oldroydi* at 10 m on rocks near Indian Rock, Santa Catalina Island, California. These mollusks were transported to Texas A&M University and kept in a refrigerated marine aquarium at 10°C. Inactive and heavily encrusted with coralline algae, the two specimens mostly went unnoticed. However, in fall 1991, a cluster of the "strawberry anemone" *Corynactis californica* Carlgren, 1936 (actually a member of the order Corallimorpharia) was added to the tank. We noticed that the *L. oldroydi* crawled to the cluster, and that bare patches appeared among the anemones.

From 27 January to 6 May 1992 we kept records of the movements of the two *Latiaxis oldroydi* and the numbers of *Corynactis californica*. During that time, the mollusks ate 16 anemones, averaging one anemone per mollusk per week (range 0-3 anemones per week). During much of the time, the mollusks remained almost motionless, but one moved 7 cm in a single day. The anemones did not present any noticeable escape responses, such as crawling on the pedal disk, detaching from the substrate, or attempting to sting, although one anemone removed itself from harm's way by attaching to the dorsal surface of a mollusk's shell.

Members of the Coralliophilidae have not been reported previously to feed on corallimorpharians. Due to its relatively strong stinging cells, *Corynactis californica* apparently has few predators. The leather starfish *Dermasterias imbricata* (Grube, 1857) will consume strawberry anemones, although it seems to prefer other species of anthozoans as prey if it has access to them (ANNETT AND PIEROTTI, 1984).

In nature, it is likely that *Latiaxis oldroydi* also feeds on the athermatypic coral *Astrangia lajollaensis* Durham, 1947, which is common in the areas it inhabits. It also may feed on the corals *Paracyathus stearnsi* Verrill, 1869, and *Coenocyathus bowersi* Vaughan, 1906, which live in subtidal rocky areas off southern California.

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**Invasion of the South Texas Coast by the
Edible Brown Mussel *Perna perna*
(Linnaeus, 1758)**

by

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Biological invasion as defined by CARLTON (1987) is the arrival, establishment, and diffusion of a species. Biological invasions in natural marine communities occur through two processes, range expansions and introductions (CARLTON, 1987). Range expansions consist of dispersal by natural mechanisms into a region where the species did not formerly exist. Introductions consist of transportation by human activity into a region where the species did not formerly exist. Introductions of exotic organisms have been linked to fouling and boring communities on ships, ballast seawater from ships, semi-submersible exploratory drilling platforms, and fisheries introductions (CARLTON, 1987). Carlton tallied the number of introduced mollusks within North America at the National Shellfisheries Association meeting in April of 1990 (CHEW, 1990). The Pacific coast of North America accommodated nearly 40 non-native species, the Atlantic coast 10 or fewer, and the Gulf coast five or fewer.

The introduction of nonindigenous species can have devastating impacts on native ecosystems. The Asiatic clam (*Corbicula fluminea* Müller, 1774), inadvertently introduced into the United States in the 1930s, has spread to 35 states, colonizing all of the major Pacific and Atlantic river drainages (BRITTON & MORTON, 1979; ISOM, 1986). *Corbicula fluminea* has since become a pest organism because of biofouling in water treatment facilities, irrigation systems, and power generating stations (KING *et al.*, 1986). Another recent account of a biological invader arriving in the United States is the zebra mussel (*Dreissena polymorpha* Pallas, 1754). This small, freshwater mollusk has the potential to spread throughout much of North America and create serious problems for various aquatic organisms, par-

ticularly native endangered mussels (FRENCH, 1990) while also biofouling various water usage facilities. The zebra mussel apparently was introduced from Europe accidentally via the release of ballast water from international vessels (FRENCH, 1990).

Small specimens (2 cm in length) of what was later determined to be *Perna perna* (Linnaeus, 1758) were first collected from the Port Aransas Jetty in February 1990, following one of the area's most severe freezes in December 1989. By December 1991 mussels had successfully colonized the intertidal zone of the jetty rocks at Port Aransas, Fish Pass (Corpus Christi Water Exchange Pass), and Port Mansfield Pass. The Port Aransas and Port Mansfield jetties are 230 km apart. In areas of noted colonization, mussel densities are as high as 50 individuals per quarter meter square. Due to mussel colony locations on jetty rocks that protect the entrances of bays, they are in good proximity to propagate themselves further into their respective bays wherever hard substrates are available.

Perna perna is common to the Atlantic coast of South America from Venezuela to Uruguay (RIOS, 1975, 1985; BAYNE, 1976), the southern coasts of Africa from Walvis Bay to Mozambique (KENNELLY, 1969), India, and Sri Lanka (VAKILY, 1989). Eleven synonyms for *P. perna* were cited by SIDDALL (1980). The genus *Perna* is characterized by the anterior position of the pedal retractor muscle, widely separated posterior retractor muscles, the absence of any anterior adductor muscle, and the often green color of the shell (RIOS, 1975; BAYNE, 1976). Because of the degree of variation in characters of taxonomic importance within the genus *Perna*, it is difficult to distinguish reliably among species without knowing from what locality they were collected (SIDDALL, 1980). *Perna perna* is described as up to 170 mm long (90 mm average) and smooth with concentric growth lines; it has a purple nacreous interior, and the ventral margin is straight with one or two teeth. The periostracum is dark brown with yellow-greenish bands near the ventral margin (RIOS, 1975, 1985). The most reliable anatomical character used to distinguish *P. perna* from other members of the genus is the presence of enlarged sensory papillae along the mantle margins (SIDDALL, 1980). Larval surveys in Venezuela indicate as many as three prominent spawning peaks for *P. perna* (VAKILY, 1989). Description of the larvae and dissoconch are given by MARTINEZ (1967).

Perna perna is a ciliary-mucoid filter feeder that occupies the littoral and sublittoral zones, where it, like the zebra mussel, attaches by means of byssal threads to a large variety of substrates (VAKILY, 1989). *Perna perna* tolerates fairly large fluctuations in salinity, adapting well in ranges of 19–44 ppt. Members of the genus *Perna* exhibit some sexual dimorphism. The sexes of truly mature animals can often be determined by the color of the gonads, milky to creamy white indicating a male and orange to red-orange indicating a female.

Cultivation of *Perna perna* has been attempted with limited success in Venezuela (BAYNE, 1976), where it is given the common name "Mexilhao." Sporadic outbreaks

of paralytic shellfish poisoning in the 1970s, resulting in human deaths, may have contributed to the decline of the fishery there (H. H. Hildebrand, personal communication).

The possible sources that could have resulted in the introduction of *Perna perna*, in addition to those previously mentioned, include the importing of live shellfish sold in local seafood markets. *Perna perna* was observed live in seafood markets in California (J. C. Britton, personal communication). Local seafood markets also import live mussels; however, only *Mytilus* spp. have been encountered. It is also noteworthy that the ships of a resident Venezuelan oil refining company, Champlin, frequent the Corpus Christi Bay area. *Perna* spp. have been previously documented as fouling organisms on the hulls of ships (CARLTON, 1987). The planktotrophic larvae of this mussel remains free-swimming for 15 to 20 days (VAKILY, 1989); thus transportation of the organism in ballast water is clearly a possibility. It is common practice for international vessels, including those from South America, to release ballast seawater in nearshore and inshore waters (Harbormaster's Office, Port of Corpus Christi Authority).

Shellfish introductions may also result in the inadvertent introduction of pathogens, algal cysts, and disease organisms of commercial mollusks (CARLTON, 1989; SHUMWAY, 1989). Toxic algal blooms occur all over the world and it appears the incidence and diversity of blooms has been increasing in recent years (SHUMWAY, 1989). There is increasing evidence that toxic species are being transported to new areas via the translocation of infected shellfish, which may result in the release of cysts or motile cells that may seed a future bloom in the area of translocation (SHUMWAY, 1989). The rate at which shellfish accumulate and release toxins is species specific and varies with season and the site of toxin storage within the animal (SHUMWAY, 1989). Besides the potential danger of introducing diseases, the remarkable adaptability of *Perna* to different environments could easily lead to undesirable changes in ecological equilibria (VAKILY, 1989).

Voucher specimens of *Perna perna*, collected from Corpus Christi, have been deposited at the National Museum of Natural History, Smithsonian Institution (USNM No. 869530) and are also present in the Corpus Christi State University Collection.

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Brooding of Larvae in *Cardita aviculina* Lamarck, 1819 (Bivalvia: Carditidae)

by

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Brooding of larvae in the Carditidae has been known since DALL (1903) reported viviparity in *Venericardia alaskana* Dall, 1903 (= *Cyclocardia crebicosata* (Krause, 1885)) and that members of the carditid subfamily Thecaliinae brood their young in a marsupium. JONES (1963) described brooding in *Cyclocardia bailyi* (Burch, 1944), *C. barbarensis* (Stearns, 1890), and *C. ventricosa* (Gould, 1850). YONGE (1969) studied brooding in *Glans carpenteri* (Lamy, 1922) and J. A. Allen (personal communication, in YONGE, 1969) reported brooding in *C. borealis* (Conrad, 1831). Brooding has been inferred in several species of the extinct genera *Venericardia* (HEASLIP, 1968, 1969) and *Vetericardiella*

(JABLONSKI & LUTZ, 1980, 1983). Here I report the brooding of larvae in *Cardita* (*Cardita*) *aviculina* Lamarck, 1819. Brooded larvae were found in a specimen (Academy of Natural Sciences of Philadelphia alcohol collection, 269882) from off Poum, southwest New Caledonia. None of the other 10 specimens in the lot contained larvae. This is the first report of brooded larvae in *Cardita*, *sensu stricto*, since all other species of *Cardita* in which brooding has been reported have been reassigned to either *Cyclocardia* or *Glans*.

The larvae are identical to what both JONES (1963) and YONGE (1969) considered the 1a stage of larval development. As JONES (1963) and YONGE (1969) considered typical of carditids, the larvae were numerous (approximately 100 individuals in *Cardita aviculina*), contained in the interlamellar space of both the right and left inner demi-branches, and were all at the same stage of development. The larvae were non-shelled, circular, undifferentiated, with an outer membrane and a very faint inner membrane. The diameter of the larvae ranged from 0.20 mm to 0.22 mm, larger than larvae of *Glans carpenteri* (0.12 mm), but smaller than those of *Cyclocardia ventricosa* (0.50 to 0.58 mm).

COAN (1977) speculated that brooding may hinder gene flow, and therefore lead to considerable morphologic variation between populations. Indeed, LAMY (1922) recognized multiple varieties of many widespread species of carditids, including four varieties of *Cardita aviculina* (*C. aviculina* occurs throughout the Indo-Pacific [LAMY, 1922], Hawaii [KAY, 1979], and the eastern Pacific [SHASKY, 1986]). However, the varieties are not allopatric, because the geographic distributions of the varieties are patchy and overlapping.

DALL (1903) suggested that all members of the Carditidae may brood their larvae, and YONGE (1969) and COAN (1977) also considered this possibility. STRATHMANN (1985) has argued that taxa with lecithotrophy (non-feeding larvae, which would include those which are brooded) are derived from taxa with planktotrophy (feeding larvae), but rarely the reverse. Brooding may then be considered either (1) primitive for the Carditidae, or (2) having independently evolved several times. Since planktotrophy is as yet unknown in the Carditidae, alternative (1) is the more likely scenario. However, this question cannot be fully resolved until more species of Carditidae are studied and the group is examined phylogenetically.

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**In Situ Spawning Behavior of an Alaskan
Population of Pinto Abalone,
Haliotis kamtschatkana Jonas, 1845**

by

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Introduction

The pinto abalone (*Haliotis kamtschatkana* Jonas, 1845) supports a small commercial fishery in southeastern Alaska, but few studies have addressed its biology in the Alaskan part of its range (LIVINGSTONE, 1952; PAUL *et al.*, 1977; PAUL & PAUL, 1981; STANDLEY, 1987). In British Columbia the species supported a much larger fishery until its closure in 1990 and has been the subject of many studies

(BREEN, 1980, 1986; BREEN & ADKINS, 1979, 1980; QUAYLE, 1962, 1971; SLOAN & BREEN, 1988).

Knowledge of the reproductive biology of the species is important for management, as fishery openings might be timed to permit reproduction prior to harvest. No clearly defined reproductive cycle was evident in gonadal sections from British Columbia specimens; however, spontaneous spawning by pinto abalone in laboratory cultures was observed (QUAYLE, 1971). An *in situ* spawning of pinto abalone was observed in mid-July in the Queen Charlotte Islands; but, because approximately 500 abalone had been handled and aerially exposed while being tagged with plastic spaghetti tags before their return to the water, a strong possibility existed that handling had induced the spawning (BREEN & ADKINS, 1980). STANDLEY (1987) extensively studied the reproductive biology of pinto abalone from Sitka Sound; she observed spontaneous laboratory spawning of pinto abalone (primarily in early summer) and was able to induce spawning by a variety of methods, but did not observe *in situ* spawning. The lack of observations of *in situ* spawning of pinto abalone is not unusual, as observations of any species of abalone spawning are rare (HAHN, 1989).

Observations

Observations of spawning abalone were made with the aid of SCUBA near the mouth of Whiting Harbor, Sitka, Alaska (57°03'15"N, 135°22'22"W) at 1730 hr on 30 July 1991. Most of the abalone observed spawning were males at between 3 and 5 m depth. The weather was overcast, with calm seas and little wind; air temperature was 13.9°C. The water column had little temperature or salinity stratification; temperature varied by less than 1°C and salinity varied by less than 1 ppt between the surface and 5 m depth, and only slightly more variation was present to 10 m depth (Table 1). Observations were made approximately one hour after high tide; currents were minimal and gametes slowly dissipated (Figure 1). Tidal ranges were intermediate between spring and neap tides. The spawning population was videotaped; 35-mm underwater cameras were also used to document the event.

Red sea urchins, *Strongylocentrotus franciscanus* (A. Agassiz, 1863), and topsnails (*Calliostoma* sp.) were the most common macrofauna other than abalone, but the sunflower star, *Pycnopodia helianthoides* (Brandt, 1835), and kelp greenling, *Hexagrammos decagrammus* (Pallas, 1810), were present.

Discussion

It is unlikely that diver activities triggered spawning, because spawning was in progress at first observation and occurred prior to any handling. MOTTET (1978) and HAHN (1989) reviewed exposure and rapid temperature changes as natural spawning stimuli for a variety of abalone species. BREEN & ADKINS (1980) suggested that tidal temperature rhythm might be a spawning stimulus for pinto abalone,

Table 1

Temperature (°C) and salinity (ppt) by depth at the time of spawning observations of pinto abalone, *Haliotis kamtschatkana*, in Sitka Sound, Alaska, on 30 July 1991.

Depth (m)	Temperature (°C)	Salinity (ppt)
0.2	13.22	29.99
1	13.17	30.01
2	13.13	30.01
3	13.05	30.04
4	12.76	30.20
5	12.64	30.30
6	12.57	30.33
7	12.13	30.76
8	12.06	30.79
9	12.00	30.83
10	11.86	30.93

explaining the spatial and temporal variability that has been reported (QUAYLE, 1971). These suggestions offer little explanation for our spawning observations. The pinto abalone observed in Sitka Sound were below the depth of

tidal exposure, the water column had little temperature stratification, and spawning was observed shortly after high tide, when the abalone would have been exposed to the smallest temperature variation.

Pinto abalone are not unusual in the variability that has been reported for their gonadal maturation and spawning periods. A wide variability in spawning times has been reported for abalone both within and between species (HAHN, 1989; MOTTET, 1978). Black abalone, *Haliotis cracherodii* Leach, 1814, populations only a few kilometers apart in California had different spawning times (WEBBER & GIESE, 1969). Similarly, *H. rubra* at different locations in Australia had vastly different spawning periods, and in different seasons (SHEPHERD & LAWS, 1974).

The spatial extent of abalone spawning on the day of our observations is unknown; however, all abalone observed at the site were spawning, including the smallest individuals. The distribution of abalone was patchy; areas of high density were interspersed with areas containing no abalone. The implication from the observed distributions is that the abalone formed many, small spawning aggregations.

The pinto abalone appeared to be climbing as high above



Figure 1

Spawning pinto abalone, *Haliotis kamtschatkana*, on stipe of *Pleurophyucus* sp. A red sea urchin is in the foreground and other abalone are visible in the background (photograph by M. Ridgway).

the bottom as possible. Most abalone were on the stipes of *Pleurophycus* sp. and *Laminaria* sp. (although some were observed on blades of *Costaria* sp. and *Macrocystis* sp.), with many abalone stacked on top of each other, up to five individuals high, with the uppermost individual being up to 1–2 m above the substrate. Interestingly, only males were observed in stacks; however, since the sexes were identified primarily by their gametes, females could have been missed. Upward vertical movements of abalone prior to spawning (primarily in laboratory culture) have been reported for numerous species (see reviews by MOTTET, 1978; HAHN, 1989), including pinto abalone (QUAYLE, 1971; BREEN & ADKINS, 1980).

BREEN & ADKINS (1980) suggested the vertical movements might be a mechanism for concentrating the adults, or alternatively, strategies for releasing gametes into the warmest water possible or for exposing eggs to the greatest amount of sperm before settling to the bottom. They argued that the adult concentrations might have strong adaptive roles, and that decreases in local density due to overharvesting might have a pronounced influence on recruitment success. LEVITAN *et al.* (1992) reported that the distribution and abundance of spawning organisms can have a profound influence on reproductive success and quantified the significance of spawning concentrations.

Our observations constitute the first published report of *in situ* spawning of pinto abalone in Alaskan waters, confirm the observations of BREEN & ADKINS (1980) made in British Columbian waters, and extend the documented spawning time of pinto abalone until late July.

Acknowledgments

We thank M. Ridgway, who made the initial spawning observations, and P. Else for their assistance with underwater photography and data collection. This project was funded by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Washington, D.C., through grant Nos. NA87AA-D-SG065 and NA16RG0167-01 to the National Coastal Resources Research and Development Institute, Portland, Oregon. Other funding was provided by the Japan Overseas Fisheries Cooperation Foundation (Japan OFCF) and the Alaska Department of Commerce and Economic Development.

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BOOKS, PERIODICALS & PAMPHLETS

The Encyclopedia of Seashells

by GARY ROSENBERG. 1992. Michael Friedman Publishing Group, Inc., New York. 224 pp. Hardcover \$20. North American distribution through B. F. Dalton and Barnes and Noble bookstores.

At first glance, this attractive mass-marketed volume has all the trappings of one more coffee-table shell book. The dust jacket is one of those arrangements of colorful shells artistically deployed in orientations and at scales that disturb the professional eye. The frontispiece is a photographic jumble of sea treasures (with as many echinoderms, cnidarians, and barnacles as mollusks, all seemingly nestled into a bed of soapsuds), and the shell on the page facing the table of contents is propped shamelessly in the swash in a seductive, pink-lipped, apertural display.

Then the author assumes control, and the tone changes. The page facing the preface is a reproduction of a hand-colored plate from Chenu's *Illustrations Conchyliologiques*, and by page 8, *voilà*, a full-page cladogram! In the disguise of a coffee-table book, Gary Rosenberg has produced an affordable scholarly reference that fills an empty niche. It offers a self-starting education in molluscan taxonomic diversity that begins with the shell, while providing the reader with some basic anatomical information, a basic technical glossary, and a geographical index to shell identification guides. Most importantly, it provides a bibliography of nearly 400 references to authoritative primary literature for the major families of shelled marine mollusks.

The author has achieved a scholarly goal in spite of what sounded like an intellectually vacuous contract charge to produce a picture book of pretty shells. Working within the constraint of selecting 250 species (one color illustration and 200 words each), Gary Rosenberg arrived at the clever subterfuge of choosing each species to represent a different family, or in some instances subfamily. The color photographs (mostly the work of the author) are outstanding, and in addition to a brief account of each illustrated species there is an informative summary of the family. In the case of two of the hydrothermal vent taxa (*Neomphalus fretterae* and *Calyplogena magnifica*) Rosenberg has photographed paratype material, although specimen data and repositories are beyond the limits of the subterfuge.

In spite of the absence of catalog numbers on any of the photographed specimens, the chapter on shell collecting presents the amateur collector or student with unusually rigorous instructions and challenges to data collection and data management. This includes a section of advice on information fields and database programs for curating personal shell collections with a home computer.

If this were intended as a technical publication or textbook, I would be tempted to critique specifics of content and omissions; but that is not appropriate here. What is

important is the appearance of a unique reference work that presents molluscan diversity systematically to the non-professional as an intellectually challenging subject and that speaks of natural history in the best sense of the tradition.

Carole S. Hickman

Eocene Mollusca from the Vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: Paleoecology and Systematics

by PHILLIP A. MAXWELL. 1992. New Zealand Geological Survey Paleontological Bulletin 65. 280 pp.; 30 plates. Paperback \$70. Publications Officer, DSIR Geology & Geophysics, P.O. Box 30 368, Lower Hutt, New Zealand. FAX (04) 5695-016.

This faunal monograph continues in the exemplary modern tradition set by New Zealand paleontologists. It provides the first comprehensive documentation of one of the most spectacular Eocene molluscan faunas in the Southern Hemisphere, recording 250 species. The monograph introduces 10 new generic names and 89 new species (18 bivalves, 64 gastropods, and 7 scaphopods). There are 42 new combinations; and the new taxa, new combinations, and new synonymies are conveniently summarized in an appendix. Separate sections provide detailed analysis of the composition of the fauna, family by family, and the paleoecology. The plates (which contain 438 photographs) are of high quality. Two distinctive faunules, both from outer shelf to upper bathyal tuff beds, dominate the monograph and will play a major role in any reevaluation of the evolution of Eocene offshore faunas.

The mollusks of classic McCulloch's bridge locality have been collected and partially described over a period of 125 years. This long-awaited and meticulously updated publication is Phil Maxwell's Ph.D. thesis, prepared approximately 20 years ago. It is indeed fortunate that this work has made it to publication in spite of the budgetary crises and the changing complexion of government science in New Zealand that has eliminated Maxwell's position and transformed the New Zealand Geological Survey first into the "Department of Scientific and Industrial Research: Geology and Geophysics," and more recently into the "Institute of Geological and Nuclear Sciences Limited" (a government "science company").

Carole S. Hickman

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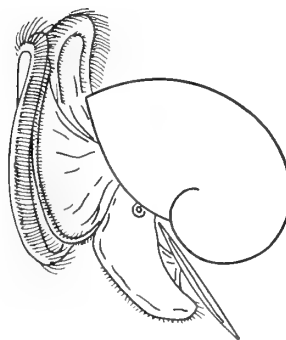
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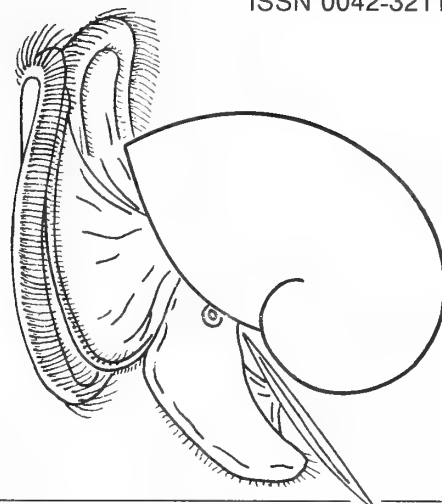
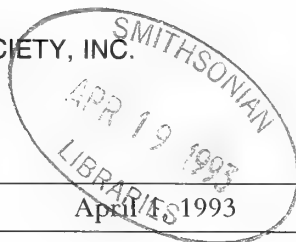
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THE VELIGER

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Population Structure of Two Common Species of Ascoglossan (= Sacoglossan) Opisthobranchs on the Central Coast of Oregon, USA

by

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Abstract. The herbivorous ascoglossan opisthobranch fauna in the N.E. Pacific has been extensively studied in terms of species diversity, geographic range, seasonality, and host-plant associations. Yet, basic demographic information is lacking for most of the local species. To fill this gap, two common species of ascoglossans were examined along the central coast of Oregon, USA: the large, conspicuous *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905) and the small, cryptic *Alderia modesta* (Lovén, 1844). Three aspects of demography were quantified: (1) population structure and size range, (2) length-weight relationships, and (3) size-specific egg mass deposition. During the summer of 1990, *Aplysiopsis enteromorphae* collected from high intertidal, saline pools at Strawberry Hill and Neptune Beach state parks, Oregon varied in size from 4 to 277 mg (wet weight). These values corresponded to body lengths of ~5 to 20 mm. Most *Aplysiopsis enteromorphae* deposited egg masses in the laboratory, and egg mass weight was unrelated to ascoglossan body size. Thus, in contrast to many other opisthobranchs, there was no apparent fecundity advantage of large size. In June 1990, *Alderia modesta* collected from high intertidal algal mats in Yaquina Bay, Oregon ranged in size from 0.4 to 13.3 mg (wet weight). Most individuals were <6 mm in length. The proportion of ascoglossans depositing egg masses was size specific: *Alderia modesta* <2 mg commonly did not produce egg masses whereas individuals >3 mg almost always deposited eggs. The minimum size of egg deposition was extremely small for both species: ≤4 mg in *Aplysiopsis enteromorphae* and <0.4 mg in *Alderia modesta*. Therefore, the majority of individuals in populations of both species were reproductively competent. Early, continuous reproduction may be a mechanism for some ascoglossans to ensure production of offspring under unpredictable conditions.

INTRODUCTION

Ascoglossan (= sacoglossan) opisthobranchs are a common, though often overlooked, group of mollusks because of their generally small size, often cryptic coloration, and patchy distribution (MILLEN, 1980). Although the biology of the ascoglossan fauna has been studied in detail for many geographic regions (e.g., N.W. Atlantic, Caribbean, N.E. Atlantic, Mediterranean), there is a comparative paucity of basic information on species in the N.E. Pacific. Even when species appear cosmopolitan, extrapolations from different geographic regions may not necessarily be reliable

because of different (1) abiotic factors (e.g., tidal patterns, water temperature, upwelling regimes) and (2) biotic factors (e.g., predators, competitors, algal host species). Regional and local information on ascoglossan populations is, therefore, merited.

Four species of N.E. Pacific ascoglossans are common: *Placida dendritica* (Alder & Hancock, 1843), *Elysia hedgpethi* (Marcus, 1961), *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905), and *Alderia modesta* (Lovén, 1844). The extent of ranges of these species and other, less common ascoglossans has been examined by many workers (LANCE, 1961, 1966; MARCUS, 1961; STEINBERG, 1963; MACFARLAND, 1966; SPHON & LANCE, 1968; ROLLER & LONG, 1969; GOSLINER & WILLIAMS, 1970; SPHON, 1971; WILLIAMS & GOSLINER, 1973; LAMBERT, 1976; MILLEN, 1980, 1989; GODDARD, 1984; FOSTER, 1987; BEHRENS, 1991).

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A. Marine, Rocky Shore

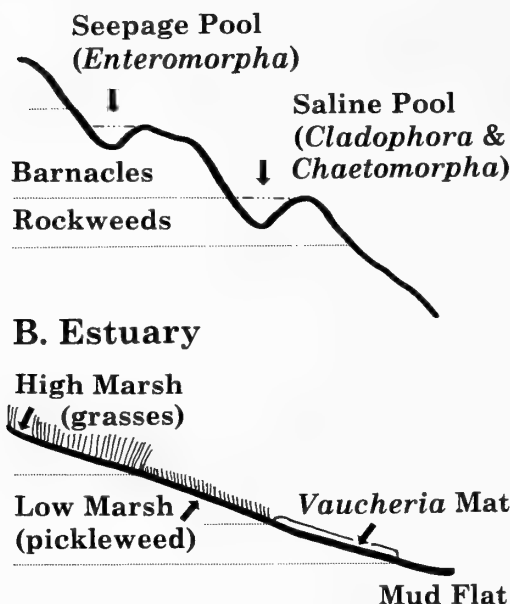


Figure 1

Profile of shores illustrating location of ascoglossan habitats. A. High intertidal, open-coast pools containing filamentous green algae (*Cladophora*, *Chaetomorpha*) with the ascoglossan *Aplysiopsis enteromorphae*. B. High intertidal, estuarine algal mats (*Vaucheria*) with the ascoglossan *Alderia modesta*.

In contrast, aspects of ascoglossan population ecology have received comparatively little attention. Detailed information is known about the population structure and dynamics of *P. dendritica* on the Oregon coast (TROWBRIDGE, 1991a, b, 1992a, b). Furthermore, more limited data on feeding, egg masses, and veligers exist (HAND & STEINBERG, 1955; GONOR, 1961; GREENE, 1968). The objective of the present study was to provide descriptive information on the population structure of two common species: *Aplysiopsis enteromorphae* and *Alderia modesta*.

NATURAL HISTORY

Aplysiopsis enteromorphae (reported primarily as *A. smithi* before BEHRENS (1991)) has a limited geographic distribution, inhabiting N.E. Pacific shores from Alaska to the Gulf of California (LANCE, 1961; ROLLER & LONG, 1969; GOSLINER & WILLIAMS, 1970; MILLEN, 1980, 1989; BEHRENS, 1991). The opisthobranch has a disjunct local distribution, occurring (1) in high intertidal, open-coast pools on filamentous green algae and (2) in bays and estuaries on green algal mats (GONOR, 1961; STEINBERG, 1963; GREENE, 1968; GOSLINER & WILLIAMS, 1970; WILLIAMS & GOSLINER, 1973; GODDARD, 1984; TROWBRIDGE, in press). Although the conspicuous ascoglossan regularly occurs in both habitats, its low density makes *A. enteromorphae*

a predictably sparse species. The ascoglossan occurs on the shore from April or May to September in Washington and Oregon (GONOR, 1961; GODDARD, 1984; TROWBRIDGE, in press) and from January to June in California (LANCE, 1961). Individuals of the species attain lengths of 2 to 3 cm (TROWBRIDGE, in press).

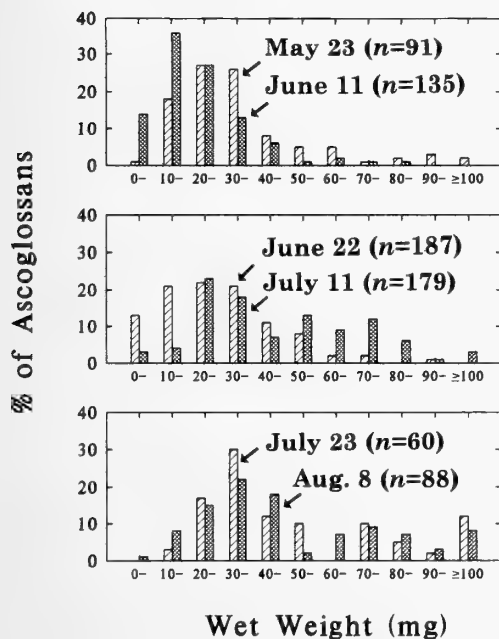
Alderia modesta inhabits temperate and boreal estuaries throughout the Northern Hemisphere (HARTOG & SWENNEN, 1952; HAND, 1955; HAND & STEINBERG, 1955; HARTOG, 1958, 1959; STEINBERG, 1963; BLEAKNEY & BAILEY, 1967; CLARK, 1975; THOMPSON, 1976; MILLEN, 1980, 1989; VADER, 1981; ROGINSKAJA, 1984). The ascoglossan occurs in association with the high intertidal, mat-forming, yellow-green alga *Vaucheria* sp. that grows within and directly downshore from salt marsh vegetation such as pickleweed (*Salicornia*) (HAND & STEINBERG, 1955; HARTOG, 1959; STEINBERG, 1963; VADER, 1981). *Alderia modesta* often forms high-density populations, ranging from tens to thousands of animals per square meter (HARTOG, 1959; SEELEMANN, 1967; VADER, 1981; TROWBRIDGE, unpublished data). Larvae of *A. modesta* settle, metamorphose, and recruit to the algal mats during spring, summer, and fall in most Atlantic localities (HARTOG, 1959; VADER, 1981). My observations of juveniles (1 to 2 mm long) in winter on Oregon mudflats indicate that the herbivore may have broader seasonality in the N.E. Pacific. *Alderia modesta* grows to sexual maturity in ~10 days after metamorphosis (SEELEMANN, 1967) and attains maximum lengths of 5 to 16 mm, depending upon locality (ENGEL *et al.*, 1940; HAND & STEINBERG, 1955; HARTOG, 1959; BLEAKNEY & BAILEY, 1967; THOMPSON, 1976).

The two ascoglossan species, therefore, exhibit a number of striking differences including breadth of geographic range, extent of habitat specificity, population density, phenology, and body size. In this study, three aspects of ascoglossan population structure were quantified: (1) size-frequency distribution and size range, (2) length-weight relationship, and (3) size-specific egg mass production.

MATERIALS AND METHODS

Collection Locations

Aplysiopsis enteromorphae was collected from filamentous green algae in high intertidal, saline pools at Strawberry Hill and Neptune Beach state parks (44°15'N, 124°7'W) on the central coast of Oregon, USA. Pools ranged in tidal level from the upper end of the acorn barnacle zone (primarily *Balanus glandula*) to the upper end of the rockweed zone (*Pelvetiopsis limitata*) (Figure 1A). *Alderia modesta* was collected from mats of the yellow-green alga *Vaucheria* sp. on the south shore of Yaquina Bay, Oregon (44°37'N, 124°3'W). The algal mats occurred directly downshore from salt marshes (Figure 1B), particularly low marshes composed of pickleweed (*Salicornia virginica*). Ascoglossans were brought back to the Hatfield Marine Science Center in Newport, Oregon for measurement.

Aplysiopsis enteromorphae

Wet Weight (mg)
Figure 2

Size-frequency distributions of *Aplysiopsis enteromorphae* in high intertidal pools at Strawberry Hill and Neptune Beach state parks, Oregon at two-week intervals in 1990. Data were pooled from the two sites. Sample sizes indicate the number of individuals weighed for each collection.

Procedures

From May to August 1990, *Aplysiopsis enteromorphae* was collected every two weeks from all available pools at the two sites. Measurements of ascoglossan size were based primarily on wet weight because it was faster to quantify and more repeatable than body length for unanaesthetized animals. Each individual was gently blotted and weighed to the nearest milligram. More accurate estimates could not be reliably made for *A. enteromorphae* because of (1) copious secretion of mucus and viscous white fluid and (2) autotomy of cerata when disturbed. In the late July sample, the body length of *A. enteromorphae* was measured to the nearest millimeter using a dissecting microscope with an ocular micrometer.

In June 1990, *Alderia modesta* was collected from three randomly placed 0.25-m² quadrats on the south shore of Yaquina Bay, Oregon. Because of the high disturbance threshold of *A. modesta*, individuals could be weighed with more accuracy, to the nearest 0.01 mg. In late July, another batch of ascoglossans was collected for a length-weight comparison. Body length was measured, as before with an ocular micrometer, to the nearest millimeter.

The size-specific egg mass production of each species

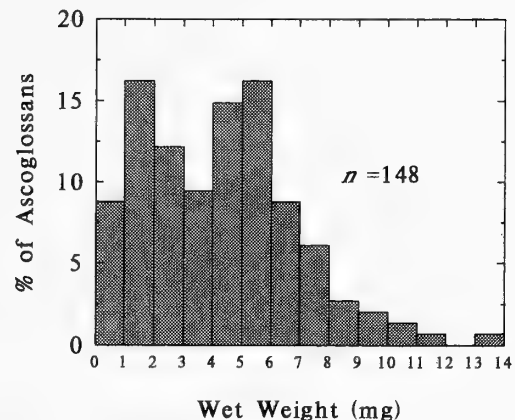
Alderia modesta

Figure 3

Size-frequency distribution of *Alderia modesta* on high intertidal *Vaucheria* mats in Yaquina Bay, Oregon in June 1990. Data were pooled from three randomly selected 0.25-m² quadrats. Sample size indicates the number of individuals weighed.

was estimated in the laboratory. Individual pre-weighed ascoglossans were placed in separate plastic petri dishes with fresh seawater. Petri dishes were set in a constant temperature room at 11°C, and the seawater was changed daily. The temperature was comparable to sea surface temperature in the field. After three days, the presence or absence of egg masses in each petri dish was noted. Egg masses of *Aplysiopsis enteromorphae* were gently blotted and weighed to the nearest milligram (wet weight). Egg masses were then dried for 24 hr at 50°C and then reweighed (dry weight). Because of the small size of egg masses of *Alderia modesta*, complementary data on wet and dry weight were not collected: most values were below the level of detection on the available balance (0.01 mg).

RESULTS

Size Structure

From May to August 1990, *Aplysiopsis enteromorphae* varied in size from 4 to 277 mg (wet weight) with a range of sizes occurring in all six biweekly samples (Figure 2). In early May, *A. enteromorphae* was not found in the pools. The sample on 23 May, therefore, was comprised of animals ≤2 weeks old. Either adult ascoglossans had migrated into the pools, perhaps from subtidal algae, or individuals had grown up to over 100 mg in the intervening period. Because virtually all the ascoglossans were removed from every available pool encountered at Strawberry Hill and Neptune Beach, the size-frequency distributions reflected primarily settlement and/or growth within each 2-week period. The distributions did vary significantly among sampling periods (*G*-test, $G = 199.0$, 20 df, $n = 740$, $P < 0.001$). Samples on 11 and 22 June had a greater

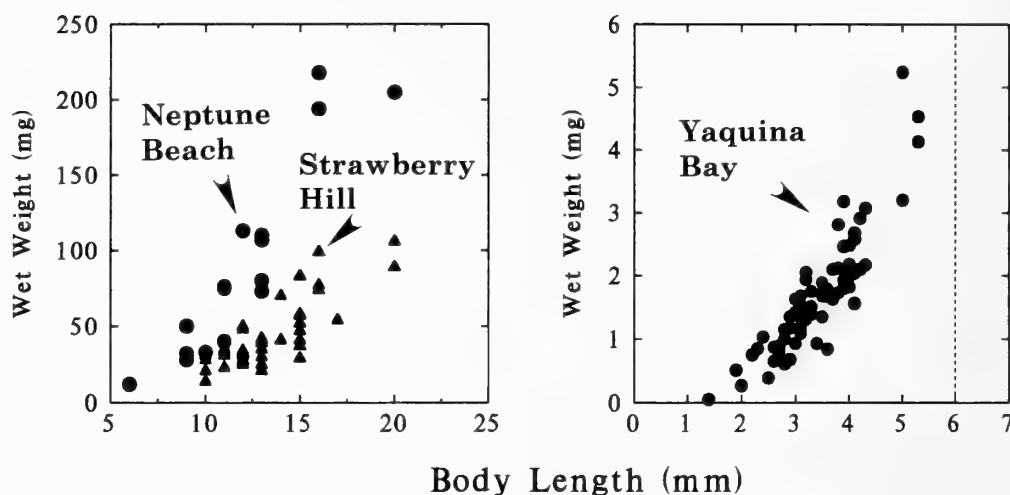
A. *Aplysiopsis*B. *Alderia*

Figure 4

Length-weight relationships for *Aplysiopsis enteromorphae* (A) and *Alderia modesta* (B) in July 1990. Collection sites are indicated. Vertical dashed line (B) indicates approximate maximum size of *Alderia modesta* in Yaquina Bay, Oregon.

A. Egg Masses

B. Fecundity

C. Precision

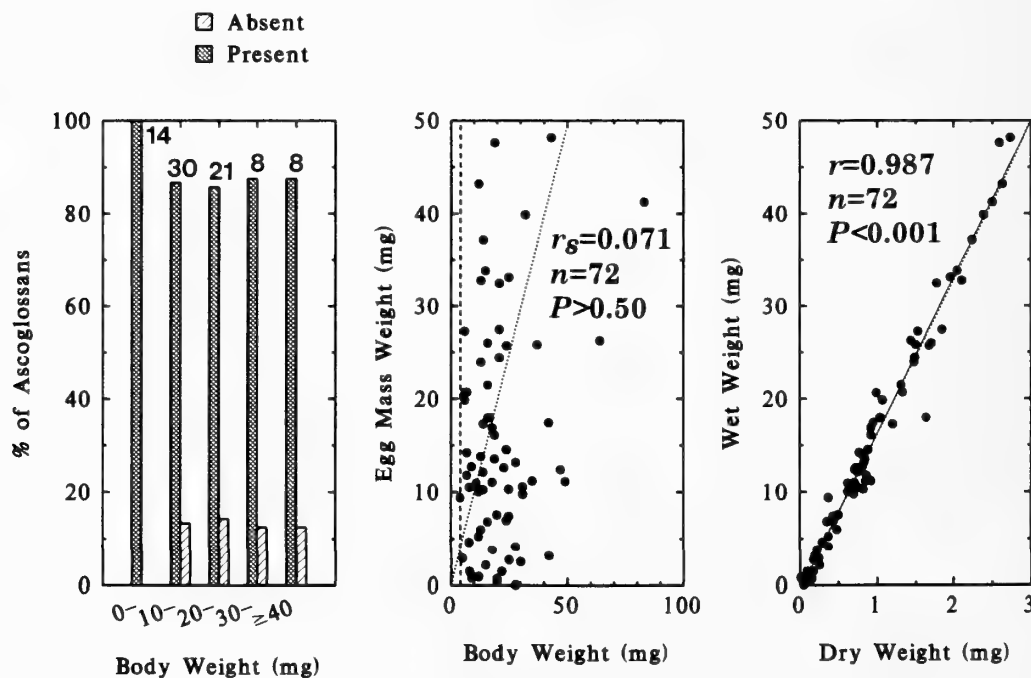


Figure 5

Egg mass production of *Aplysiopsis enteromorphae* in the laboratory (3 days, 11°C). A. Percentage of ascoglossans producing egg masses (n denotes number of individuals measured). B. Scatter plot of egg mass and ascoglossan body weight. Vertical dashed line indicates the minimum size of egg mass production; dotted line indicates the 1:1 ratio of egg mass to body weight. C. Correlation of wet and dry weight of 72 *A. enteromorphae* egg masses.

Table 1

Regression equations relating body length (mm) and wet weight (mg) of *Aplysiopsis enteromorphae*: $\log_{10}(\text{weight}) = m \cdot \log_{10}(\text{length}) + b$, such that m and b are constants. The symbol n indicates the number of ascoglossans measured. The coefficient of determination, r^2 , indicates the proportion of the variation accounted for by the regression line whereas the F and P values evaluate the statistical significance of the line.

Sites	m	b	n	r^2	F	P
Neptune Beach	2.656	-2.265	16	0.885	107.9	<0.001
Strawberry Hill	1.945	-1.321	44	0.611	65.9	<0.001
Two sites pooled	1.868	-0.913	60	0.434	44.5	<0.001

proportion of ascoglossans <20 mg than did other samples: thus, recruitment appeared to be concentrated in June.

Alderia modesta was a much smaller ascoglossan, ranging in size from 0.35 to 13.30 mg (wet weight) in the June 1990 collection (Figure 3). Although skewed to the left, the size-frequency distribution appeared bimodal with small animals (1–2 mg) and larger conspecifics (4–6 mg) being the most common. On a local scale, however, *A. modesta* populations varied: size-frequency distributions of three randomly placed quadrats differed significantly (G -test, $G = 42.0$, 6 df, $n = 148$, $P < 0.001$). Although the sources of the ascoglossan size variation were not specifically addressed, *A. modesta* tended to be much larger and more abundant on lush, dark green, velvety *Vaucheria* mats and smaller and less abundant on tough, hardened mats. Thus, herbivore size variation may reflect differences in quality of the local algal mat as food and substratum. Due to the substantial spatial variation, seasonal collections were not made: temporal variation in population structure would be obscured by high spatial variation.

Length vs. Weight

When two collections of *Aplysiopsis enteromorphae* from different sites were examined, the length-weight relationships differed (Figure 4A). At Neptune Beach, ascoglossans were much heavier for a given body length than conspecifics at Strawberry Hill (ANCOVA, $F = 93.0$, $P < 0.001$ on log-transformed data). When each site was considered separately, weight was directly related to body length (Table 1, $P < 0.001$). When data were pooled (Table 1), the relation was still significant although the association was more variable ($r^2 = 0.434$, $P < 0.001$). Based on size-frequency distributions and length-weight relations, the majority of individuals present during the summer were between 10 and 20 mm in length.

For *Alderia modesta* (Figure 4B), wet weight was directly related to length (linear regression on log-transformed data, $r^2 = 0.866$, $n = 148$, $F = 945.5$, $P < 0.001$). Thus, modal sizes of *A. modesta* (Figure 3) corresponded to body lengths of 3–4 mm and 5–6 mm. Although the size data were based

Alderia modesta

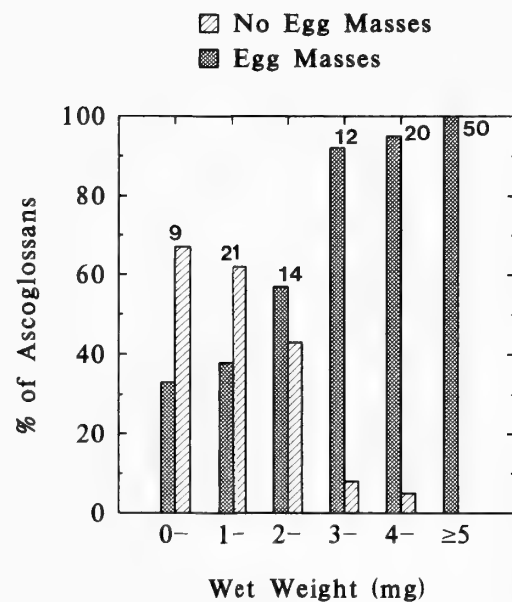


Figure 6

Percentage of *Alderia modesta* producing egg masses in the laboratory (3 days, 11°C). Numbers above each bar denote number of individuals measured.

on two collections (June and July 1990), the documented size range encompassed the observed range during other times of the year. Based on the asymptote for body length at ~6 mm (Figure 4B), maximum size of *A. modesta* in Yaquina Bay, Oregon was estimated as 6 mm.

Reproduction

The majority of *Aplysiopsis enteromorphae* produced egg masses in three days, irrespective of body size (Figure 5A). Even the smallest individual examined (4 mg wet weight) produced an egg mass in the laboratory. Furthermore, the weight of egg masses produced by each individual was clearly unrelated to ascoglossan size (Figure 5B, Spearman rank correlation, $r_s = 0.071$, $n = 72$, $P > 0.50$). The lack of size-specific fecundity was not due to the imprecision of measuring wet weight: wet and dry weight values were highly correlated (Figure 5C, Pearson correlation, $r = 0.987$, $n = 72$, $P < 0.001$).

Alderia modesta also deposited egg masses in the laboratory. The proportion of individuals producing egg masses, however, was size specific (Figure 6). Most individuals <2 mg did not deposit eggs whereas almost all the ascoglossans >3 mg did. The minimum size of egg deposition was small: even the smallest *A. modesta* examined (0.45 mg) produced egg masses.

The wet weight of *Aplysiopsis enteromorphae* egg masses was high, often exceeding that of the herbivore (Figure 5B). This result suggests that the egg masses were hydro-

philic, absorbing water upon deposition. In fact, about 94% of the egg mass wet weight was composed of water or other fluids (calculated from Figure 5C). In contrast, the egg masses of *Alderia modesta* appeared not very hydrophilic: most masses weighed <0.01 mg (level of detection), even for ascoglossans weighing several milligrams.

DISCUSSION

Life-History Attributes

Opisthobranch life-history strategies have been categorized as opportunistic (= exploitist) or equilibrium (MILLER, 1962; NYBAKKEN, 1974; CLARK, 1975). Many ascoglossan species belong to the former group (CLARK, 1975). Specific opportunistic attributes include continuous recruitment, rapid growth, small size of reproduction, continuous reproduction, and short life-span. The two species studied in Oregon apparently exhibit these traits.

The rapid growth of *Aplysiopsis enteromorphae* can be estimated from the size-frequency distributions (Figure 2). If we make the simplistic assumption that modal size represents ascoglossan growth in the preceding two weeks, then a rough estimate of the species' growth rate would be ~10 mg/week or ~1.4 mg/day. This value is similar to the rate of 1.7 mg/day estimated for large (10 to 80 mg) *A. enteromorphae* in the laboratory on *Chaetomorpha* (Trowbridge, unpublished data). Smaller animals presumably grow faster.

These growth data suggest that *Aplysiopsis enteromorphae* becomes sexually mature within a few days of metamorphosis. Although the growth rate of *Alderia modesta* was not determined for Oregon populations, SEELEMANN (1967) reported that individuals from European populations grew to sexual maturity (3 mm) in 10 days after metamorphosis. The minimum size of sexual maturity noted in this study (0.4 mg \approx 2 mm, Figure 4) was comparable. Early maturation has been reported for other ascoglossans as well. For example, *Ercolania fuscata* matured in <3 weeks at ~1 mg (CLARK, 1975), and *Placida dendritica* matured at <1 mg (TROWBRIDGE, 1992b). Early, continuous egg production may ensure that most individuals produce offspring in spite of variable environmental conditions.

Pool-Dwelling Ascoglossans

Ascoglossan-algal associations exhibit striking parallels throughout temperate areas of the world. High intertidal pools with the green algae *Cladophora* and/or *Chaetomorpha* are occupied by *Aplysiopsis enteromorphae* in the N.E. Pacific, *Stiliger felinus* (Hutton, 1882) in New Zealand, and *Limapontia capitata* (Müller, 1773) and *L. senestra* (Quatrefages, 1844) in the N.E. Atlantic (reviewed by TROWBRIDGE, in press). These species have a number of important similarities: they inhabit similar habitats, feed

on the same algal genera, and exhibit conspicuous rather than cryptic coloration.

At first glance into a tidepool, *Aplysiopsis enteromorphae* may be mistaken for littorines and small mussels because of the black body with white highlights (Trowbridge, personal observations). ROGINSKAJA (1984) made a similar observation, reporting that the black *Limapontia capitata* and *L. senestra* were conspicuous against the green algal hosts and looked superficially like young periwinkles and mussels. Finally, GARSTANG (1890) remarked that the black coloration of *L. capitata* "renders it at once noticeable" (p. 422). The role of the black pigmentation is not clear. Perhaps it protects the ascoglossans from high light intensities, particularly ultraviolet radiation, in high intertidal habitats. Ascoglossan species with black pigmentation generally have non-functional chloroplasts (CLARK *et al.*, 1990), in contrast to the chloroplast symbiosis characteristic of many cryptic species. Because cladophoralean algae (*Cladophora* and *Chaetomorpha*) are structurally not suitable for chloroplast symbiosis (CLARK *et al.*, 1990), the acquisition of black pigmentation in these high intertidal species was probably not constrained by chloroplast functionality.

Two major differences, however, occur among these pool-dwelling species: body size and developmental mode. *Aplysiopsis enteromorphae* grows to 20 or 30 mm long (TROWBRIDGE, in press). In contrast, *Stiliger felinus* grows to 10 mm (POWELL, 1979), *Limapontia capitata* to 4 mm, and *L. senestra* to 8.5 mm (COLGAN, 1911; JENSEN, 1975; ROGINSKAJA, 1978). Thus, *A. enteromorphae* is considerably larger than its ecological counterparts. Furthermore, three of the species have planktotrophic larvae, whereas *L. senestra* has direct development (ROGINSKAJA, 1978; THOMPSON, 1976). Direct development would be advantageous for a high intertidal, pool-dwelling herbivore because the species could form dense local populations on green algal hosts in individual pools or on emergent substrata. ROGINSKAJA (1978) suggested that this advantage of direct development may explain why the species is widely distributed throughout the Barents and White seas. In contrast, planktotrophic larvae may have difficulty gaining access to the pools due to limited submergence time. For example, GARSTANG (1890) found *L. capitata* in pools that received fresh seawater (and, hence, larval ascoglossans) only during spring tides; the pools often dried up during neap tides.

Algal-Mat Ascoglossans

In high intertidal, estuarine environments, two ascoglossans are ecologically similar: *Alderia modesta* and *Limapontia depressa* Alder & Hancock, 1862. They inhabit *Vaucheria* mats (ENGEL *et al.*, 1940; HARTOG, 1959; VADER, 1981), feed on the alga, are small, and are usually cryptically colored (but see HARTOG [1959] for a review of color variation in *L. depressa*). *Alderia modesta* is <8 mm in the N.E. Pacific (HAND & STEINBERG, 1955; Trow-

bridge, this study) and <16 mm on North Atlantic shores (ENGEL *et al.*, 1940; HARTOG, 1959; BLEAKNEY & BAILEY, 1967; THOMPSON, 1976). *Limapontia depressa* is typically <6 mm long (THOMPSON, 1976).

The egg mass sizes of *Alderia modesta* and *Limapontia depressa* overlap considerably (HARTOG, 1958) although the sizes of the adults producing the egg masses were not given. HAND & STEINBERG (1955) reported that egg masses of *A. modesta* were up to 5.5 mm long and the maximum size of the ascoglossans was 8 mm. Thus, the species deposits egg masses of $\leq 69\%$ of its body length. Furthermore, the fecundity of this species can be high: ~ 1000 eggs/day (SEELEMANN, 1967).

Conclusions

The N.E. Pacific *Aplysiopsis enteromorphae* is a large, black ascoglossan, often considerably larger than its ecological counterparts on other temperate shores. In contrast, *Alderia modesta* in Oregon is comparable in size to conspecifics from other geographic localities and to its counterpart, *Limapontia depressa*. On the basis of literature reports and the data presented herein, both species exhibit rapid growth rates and high fecundity. By comparing and contrasting species within each ascoglossan-algal assemblage, insight will be gained as to the ecological and environmental constraints affecting ascoglossan populations.

ACKNOWLEDGMENTS

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Fine Structure of the Three Cell Types Found in the Digestive Gland of *Elysia viridis* (Opisthobranchia: Sacoglossa)

by

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Abstract. Three types of differentiated cells can be identified in the digestive gland (hepatopancreas, liver) of adult *Elysia viridis* (Montagu, 1804) with the aid of an electron microscope: digestive cells, microvilli cells, and cells with concentric-layered vacuole bodies. The last are called the “third cell type” in this study. The digestive cell, which has been the subject of many recent studies, contains chloroplasts derived from the food alga *Codium fragile*. The microvilli cell possesses a profuse and uniform brush border. The level pilose surface shows what appear to be pinocytotic invaginations, and apically the cytoplasm is interspersed with a large number of what are presumed to be pinocytotic vesicles. Large vacuoles containing osmiophilic granules occur in the basal half of the cell and sometimes seem to merge. The third cell type is described for the first time in a sacoglossan (although in pulmonate species the corresponding lime or calcium cell is common). Most of this cell is occupied by one or more vacuoles containing concentric layers of alternating electron-dense and electron-translucent material. These characteristic vacuoles are surrounded by copious rough endoplasmic reticulum.

INTRODUCTION

The digestive gland (hepatopancreas, liver) of *Elysia viridis* (Montagu, 1804) is a much-branched organ ramifying through every part of the body and ending blindly with innumerable small tubules directly under the epidermis. The relationship between the digestive gland and the green color of the slug was recognized early. SOULEYET (1852) noticed that the green substance found in the cells of the digestive gland of *Elysia* resembled the pigmentation of lower plants and DE NEGRI & DE NEGRI (1876) were able to substantiate this observation with experiments. KAWAGUTI & YAMASU (1965) and TAYLOR (1968) were the first to show that the coloration of *Elysia viridis* is actually attributable to the ingested chloroplasts of the slug's food, a siphonaceous alga. Since these studies, a large number of investigations have focused on various functional aspects such as the metabolic and photosynthetic processes of the digestive gland of *Elysia*. These have been summarized in HÖFELMEIER (1985).

Histological studies on the digestive gland of *Elysia viridis* began with HENNEGUY (1925). FRETTER (1940), in a study on the structure of the gut in three sacoglossans,

confirmed HENNEGUY's (1925) observations on *Elysia* and described extensively one cell type of the single-layered, endodermal epithelium, which she named “digestive cells.” It is the contents of these cells which give the slug its green color. A second cell type was briefly mentioned, but not clearly characterized. TAYLOR (1968), in a fundamental study of the ultrastructure and histochemistry of *Elysia viridis*, referred to FRETTER's (1940) paper, confirmed the two cell types, and termed them “digestive cells” and “lime cells.” Recent reexamination of the fine structure of the digestive gland of *Elysia viridis* has revealed important disparities with the previously mentioned results and also with the results of the more recently published investigation by GRAVES *et al.* (1979) on the digestive gland of *Elysia chlorotica*.

Few authors have worked on the fine structure of the digestive gland of the other opisthobranch orders: SCHMEKEL & WECHSLER (1968) showed four cell types (including an undifferentiated cell type) in the digestive gland of *Trinchesia granosa*. This means that I will be comparing my results chiefly with the findings of studies on the histology and ultrastructure of the digestive gland in proso-

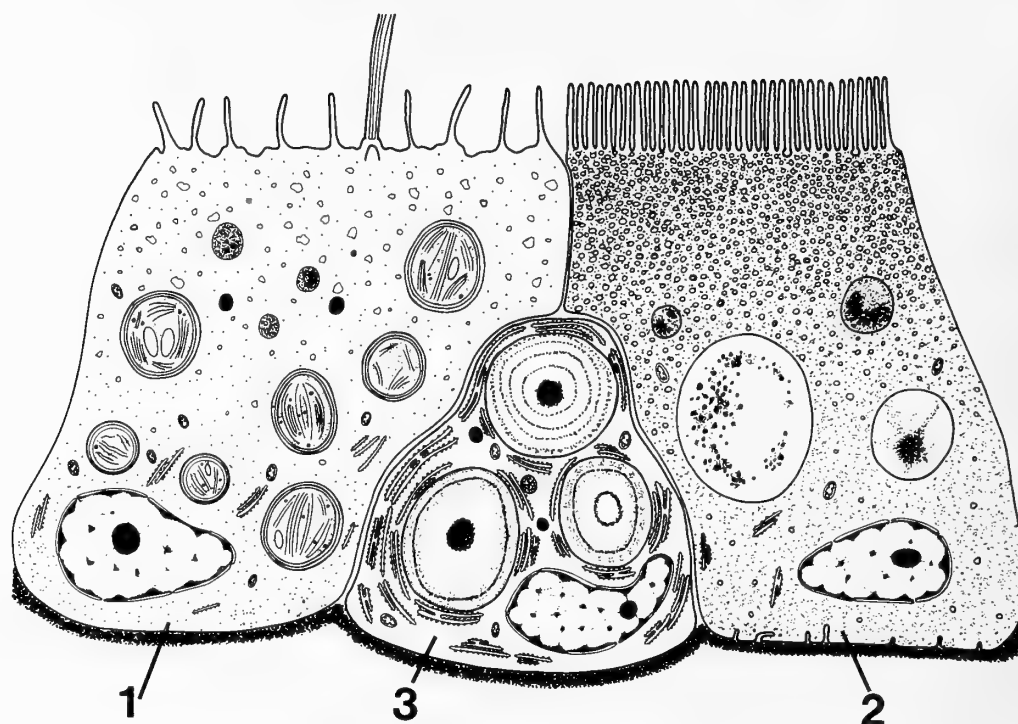


Figure 1

Diagram of the fine structure of the three cell types forming the epithelium of the digestive gland of *Elysia viridis*: the digestive cell (1), the microvilli cell (2), and the third cell type (3).

branch and pulmonate gastropods, beginning with early authors, BARFUTH (1883), HIRSCH (1917), KRIJGSMAN (1928) and THIELE (1953), and dealing in particular with the more recent authors, ABOLINŠ-KROGIS (1961, 1965, 1970), BANI (1962), SUMNER (1965, 1966a, b), WALKER (1970), and REYGROBELLET (1970).

MATERIALS AND METHODS

Specimens of *Elysia viridis* were collected on *Codium fragile* from the Mediterranean at Banyuls-sur-mer (France) and from the Atlantic coast at Roscoff (France). Before fixation, all 23 animals (length 2–15 mm) were anaesthetized for 1 to 3 hr with 7% magnesium chloride in distilled water.

The fixative used for routine light microscopy was Bouin's fluid. After fixation, the material was dehydrated and embedded in paraffin. Sections were cut at 5, 6, or 7 μ m and stained with either Heidenhain's azan, Giemsa, Masson's trichrome sequence, or Goldner's triple sequence.

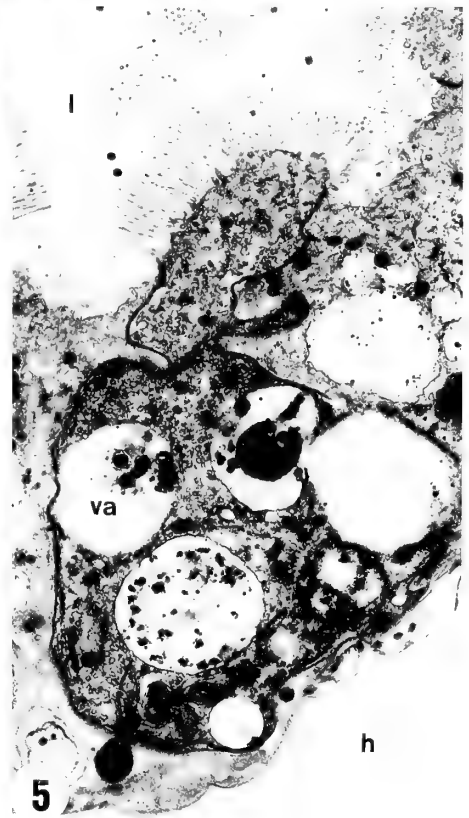
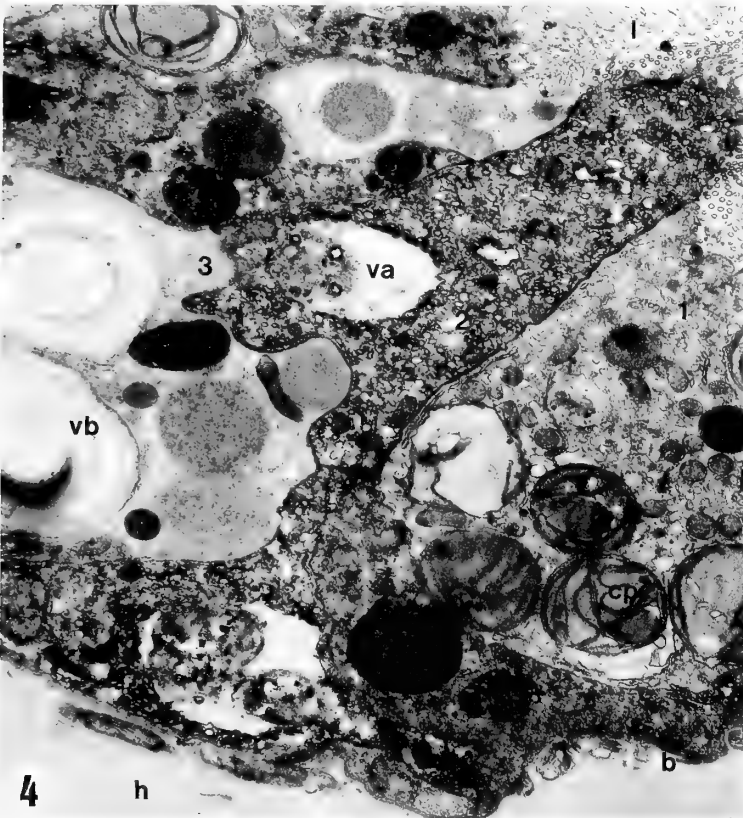
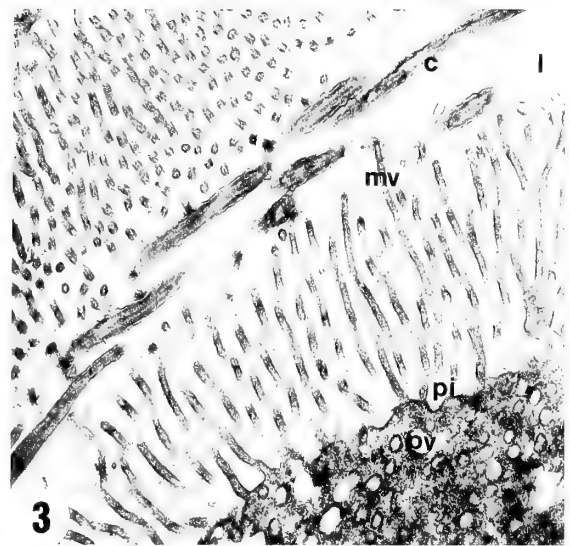
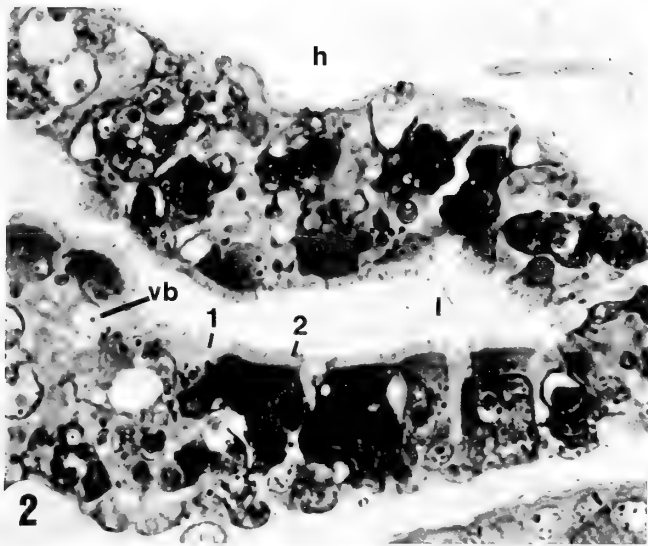
For electron microscopy, two fixation methods were used. Specimens were fixed either (1) in a solution of 0.5% potassium dichromate, 2% osmium tetroxide, and 70% double-filtered seawater, buffered to pH 7.2, or (2) 2.5% glutaraldehyde in Sørensen's phosphate buffer, followed by washing in Sørensen's phosphate buffer and postfixa-

tion in 2% osmium tetroxide in 1.25% sodium hydrogen carbonate (CLONEY & FLOREY, 1968).

After dehydration in graded series of acetone or ethanol with propylene oxide, specimens were embedded in Durcupan. Sections of 1 μ m, cut on an LKB Ultratome, were stained with 1% aqueous toluidine blue-1% aqueous borax solution at 80°C and used in the light microscope, often under phase-contrast for orientation. Sections of 600–900 Å, cut as noted before, were mounted on grids, stained with lead citrate following the procedure of REYNOLDS (1963), and then examined under a Philips EM 201 electron microscope. Micrographs were taken at magnifications from 500 to 24,000 times and enlarged photographically to the required size.

RESULTS

The digestive gland of *Elysia viridis* consists of a single-layered epithelium bounded by a thin (0.5 μ m) basal lamina and supported by connective tissue and muscle fibres. The epithelium is composed of three different cell types: the digestive cell, the microvilli cell, and a third type of cell. The three types are readily told apart under the electron microscope (Figure 4), by their position, their shape, the presence of microvilli or cilia, and by their cell content. All three cell types are found both in the main ducts of the digestive gland and in the epithelia of the small tubules



Explanation of Figures 2 to 5

Figure 2. Part of a transverse section through a digestive gland tubule composed of digestive cells (1), microvilli cells (2) with striking dense brush border, and the third cell type. Haemocoel (h); lumen of the digestive gland (l); concentric-layered vacuole body (vb). $\times 260$

Figure 3. Electron micrograph of portions of the brush border and the apical region of a microvilli cell and the cilia of the digestive cell, in longitudinal sections. Cilium (c); lumen (l); microvillus (mv); pinocytotic (?) invagination (pi); pinocytotic (?) vesicle (pv). $\times 13,000$

Figure 4. Electron micrograph of the three cell types of the epithelium of the digestive gland: digestive cell (1) with chloroplasts (cp), microvilli cell (2) with large vacuoles (va), and the third cell type (3). Basal lamina (b); concentric-layered vacuole body (vb); haemocoel (h); lumen (l). $\times 6800$

Figure 5. Electron micrograph of a microvilli cell; note the dense brush border and the content of the large vacuoles (va). Haemocoel (h); lumen (l). $\times 4500$

near the epidermis, but they do not display a uniform distribution.

The Digestive Cell

The digestive cell predominates in the epithelium of the digestive gland. It is easily recognized by the presence of chloroplasts, which are derived from the food of the slug and are found exclusively in this cell type. The digestive cell (Figures 1, 4) has a variable shape. Rectangular or triangular in outline, it averages about 9 μm in height and 14 μm in width. The apex of the cell protrudes into the lumen of the tubule or is level with the apices of the epithelium, showing small, irregular indentations.

The luminal border possesses an unkempt array of microvilli (4–5 microvilli per μm of the plasmalemma) and bears long cilia (type 9+2). Usually only one cilium per digestive cell is present in section. Longitudinal or transverse sections of cilia are frequently observed in the lumen of the tubule (Figures 2, 3). The nucleus, which is oval or kidney shaped and sometimes deeply lobulated, measures roughly 4.5 μm in length and 2 μm in width. It lies much closer to the base than to the tip of the cell and has a distinct nucleolus. The double membrane, karyolymph, and chromatin are easy to recognize. The elongate mitochondria (averaging 1 μm by 0.4 μm) with cristae and the rough endoplasmic reticulum are common, the latter usually near the base of the cell. Apically, the vacuolized cytoplasm contains many irregularly shaped vesicles; in the basal half of the cell, the cytoplasm is denser.

Many digestive cells also contain some round or oval vacuoles of various sizes and appearances. There are small, electron-dense vacuoles (0.4 to 1.7 μm in diameter), larger, clearer vacuoles (1 to 3.5 μm in diameter) with homogenous contents or small osmiophilic granules, and irregularly shaped, electron-transparent vacuoles which appear “empty.” These could also be extremely degenerated chloroplasts. It is presumed that there are transitional forms.

The round or oval-ellipsoid chloroplasts (Figure 4), measuring 1.5 to 4.5 μm in length and 1.1 to 4.3 μm in width, are bounded by a double membrane. Internally, they display a distinct lamellar structure. Apart from these lamellae, the clear homogenous matrix contains between one and eight small, round or oval granules, the so called plastoglobuli. Up to a third of the contents of a chloroplast may be taken up by the large, round or oval starch grains.

The Microvilli Cell

The microvilli cell (Figures 1, 2, 4, 5) is less common, usually rectangular in shape and averages about 11 μm by 9 μm . It lies with a broad level surface next to the lumen of the tubule of the digestive gland. This border to the tubule lumen shows a characteristic profuse, well-defined and uniform array of microvilli (Figure 3). The length of the microvilli varies from 1.6 to 2.5 μm , but the microvilli of any one cell are always of equal length. The microvilli stand close together (8 or 9 microvilli per μm of the brush border) neither branching nor intermeshing.

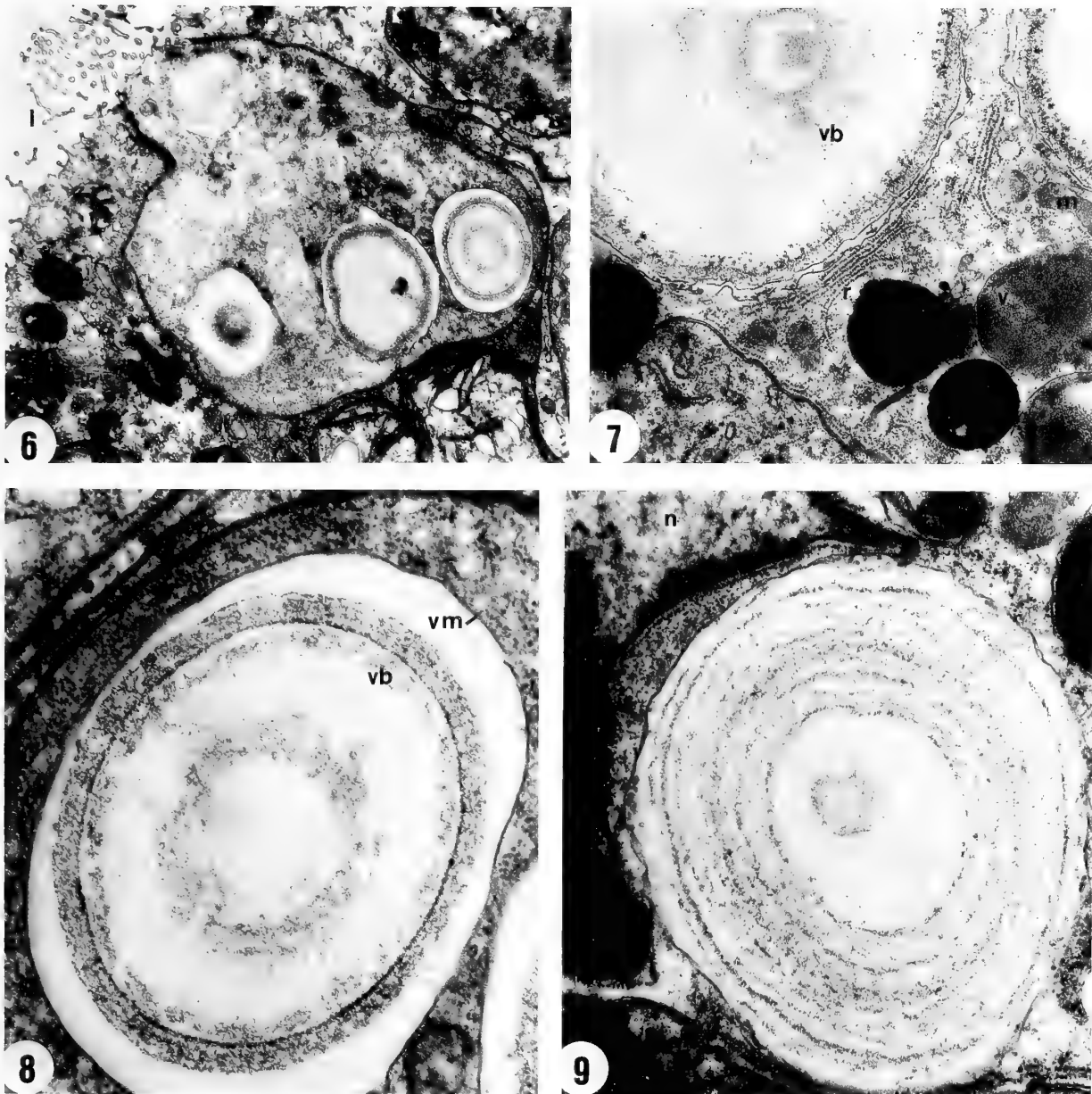
Microvilli cells are devoid of cilia. The nucleus lies in the middle of the cell or towards the base. Mitochondria are present, and rough endoplasmic reticulum is usually distributed in the basal half of the cell. The microvilli cell typically has a dark “stained” cytoplasm. This is interspersed with numerous small, round vesicles, presumably pinocytotic vesicles (Figure 3), below the luminal border in the apical region. The characteristic pinocytotic invaginations are frequently observed. Lower down the cell, fewer and larger vesicles are scattered through the cytoplasm.

Two kinds of vacuoles are found in the microvilli cell (Figure 5): large, spherical or ellipsoid vacuoles, measuring 2.8 to 6.5 μm in diameter or length, and small, round vacuoles, measuring 0.4 to 1.3 μm in diameter. In sections, the bigger vacuoles usually occur in groups of three to five if medium-sized, or one to two if large-sized; the latter take up one-half to two-thirds of the cell volume. These vacuoles always have a distinct membrane, but diverse contents: a variable number of electron-opaque granules (averaging 1 μm in diameter) may be scattered about the vacuole, which otherwise seems to be empty; other vacuoles display an accumulation of flaky, electron-dense material with no more than a few granules. The small vacuoles are densely packed with fairly uniform, electron-dense material containing a quantity of strongly osmiophilic granules. Occasionally, larger vacuoles may be observed that contain globules the size of the small vacuoles described above. These globules vary a great deal in electron density, ranging from very compact to almost dispersed. Fusions of the large vacuoles may also occur.

The Third Cell Type

The third cell type (= “lime cell”), the rarest cell type in the epithelium of the digestive gland (Figures 1, 4, 6), occurs singly or in pairs. In sections, they are triangular or rectangular in shape and average 7 μm high and 11 μm wide. The base of the cell lies broadly on the basal lamina, and the tip, while directed towards the tubule lumen, does not always actually reach it. Cells of this third type seem to be displaced into the corners of the tubules of the digestive gland, occasionally protruding with a domed outline into the haemocoel. The apical surface of the cell, very rarely seen in sections, bears microvilli (Figure 6).

The third cell type is characterized by the presence of large, clear vacuoles (Figures 7–9) occupying almost the entire cell volume. The vacuoles vary between 2 and 5 μm in diameter. They are mostly spherical, sometimes ellipsoid, and are bounded by a unit membrane. The vacuoles contain a vacuole body (\approx spherite of ABOLINŠ-KROGIS [1961, 1965, 1970], \approx spherule of SUMNER [1965, 1966a]) of electron-dense material with varied density and distribution which displays a conspicuous and characteristic concentric structure. The material lies directly beneath the unit membrane of the vacuole, or there may be a space between them. This can vary in extent from one vacuole to another but in any one vacuole the space around the



Explanation of Figures 6 to 9

Figure 6. Electron micrograph of the third cell type reaching the lumen of the digestive gland (l) and containing three different concentric-layered vacuole bodies. $\times 7500$

Figure 7. Electron micrograph of a portion of the third cell type showing rough endoplasmic reticulum (r), which surrounds the vacuole with a concentric-layered vacuole body (vb); mitochondrion (m); vacuole or vesicle (v). $\times 16,000$

Figure 8. Electron micrograph of a vacuole with concentric-layered vacuole bodies; note the space between the vacuole membrane (vm) and the vacuole body (vb). $\times 37,000$

Figure 9. Electron micrograph of a vacuole with concentric-layered vacuole body showing regular rings of electron-dense material and a spherical center. Nucleus of the third cell type (n). $\times 28,000$

vacuole body is always constant. Further investigations on live specimens will be necessary in order to establish whether this space is natural or artificial.

The material of the vacuole body may consist of alternating electron-dense and translucent zones which appear

as uniform, more or less concentric rings (Figure 9). Or, within the membrane, there may be a number of diffuse rings lying close together, circumscribing a well-defined osmiophilic circle. In a third alternative, the material may consist of irregularly distributed flakes.

The central part of the vacuole body appears either empty (Figure 8)—the contents possibly having been torn out during sectioning—or contains a compact, spherical core which may or may not have distinct edges (Figures 6, 7, 9). In some vacuole bodies the rings, circles, and spherical cores may be excentrically shifted or less uniformly structured than in the above description. Some vacuole bodies even display two cores. In any one cell, the spherules can vary in size and appearance. Occasionally, I found vacuoles of normal size (2–5 μm) but lacking entirely a concentric-layered structure, and containing only a mixture of translucent, fine, and electron-dense flaky material.

The vacuoles with concentric-layered vacuole bodies are always surrounded by rough endoplasmic reticulum (Figure 7) which may be so abundant as to fill most of the cytoplasm. This cytoplasm is, in comparison with that of the digestive and microvilli cells, very clear and frequently uniform. The nucleus lies towards the base and presents a structure resembling that of the other two cell types. The shape of the nucleus seems to fit neatly into the space not occupied by the vacuoles. Thus, sometimes a sickle-shaped or club-shaped nucleus snuggles up closely to a vacuole. The extent of the Golgi apparatus of the third cell type is not yet known.

Mitochondria are common in the third cell type. And there are also small “pigment(?)” vacuoles or vesicles averaging about 0.3 to 1 μm in diameter or length (Figure 7). These are often round (rarely oval) in shape and contain either amorphous, completely electron-dense material or weakly osmiophilic material with granules in it enveloped in a distinct membrane.

DISCUSSION

The epithelium of the digestive gland of *Elysia viridis* is composed of cells of three distinct types—digestive cells, microvilli cells, and the third cell type, *i.e.*, cells with concentric-layered vacuole bodies. (A possible embryonic or undifferentiated cell is not considered in the present paper.) This calls into question the results of FRETTER (1940), TAYLOR (1968), and GRAVES *et al.* (1979), all of whom found only two cell types in the digestive gland of *Elysia*.

One hypothesis is that we are confronted here not with different cell types, but with different phases of the cell cycle of a single cell type, as reported by GRAHAM (1938) for the three aeolids *Eolidina alderi*, *Facelina drummondi* and *Cratena glotensis*, by SUMNER (1965, 1966a, b) for *Helix aspersa*, *Succinea putris*, *Testacella mangei* and *Anodonta anatina*, and by REYGROBELLET (1970) for *Limax maximus*. My investigations on *Elysia* do not support this phase theory.

Digestive cells, which are the most plentiful type, accumulate chloroplasts derived from the food of *Elysia*, the green alga *Codium fragile*. Here, they are in part digested and in part used in photosynthesis. Since the digestive cell and particularly their chloroplasts have been the object of

many studies over the last twenty years, a more detailed discussion of the function of this cell type would be superfluous.

Homologies of the digestive cell are not difficult to find: “Leberzelle” of BARFUTH (1883), “digestive cell” of FRETTER (1940) and TAYLOR (1968), and “B-Zelle (Verdauungszelle)” of SCHMEKEL & WECHSLER (1968). The digestive cell bears apically a small number of large cilia, as observed by HENNEGUY (1925), and several microvilli. The nucleus lies towards the base and has a distinct nucleolus. These observations have already been reported by FRETTER (1940) and TAYLOR (1968).

FRETTER (1940), examining live specimens, also reported observing brown or yellowish granular clumps contained in vacuoles below the distal ends of most digestive cells. She regarded them as excretory masses, which are released from the cells and then passed through the ducts of the digestive gland to the intestine and thence to the anus, where they are expelled. TAYLOR (1968) also noticed these brown or yellowish vacuoles in living cells and, under the light microscope, described them as being filled with an amorphous substance. In electron microscopy he found, close to the basal lamina, large, clear, apparently completely empty vacuoles surrounded by complexes of rough endoplasmic reticulum. He suggested that the emptiness could be the result of extraction during the preparation of the slugs. I found no such “empty” vacuoles in the digestive gland of *Elysia*. Obviously, FRETTER’s (1940) cell with brown or yellowish vacuoles is analogous to my second cell type, the microvilli cell, and TAYLOR’s (1968) vacuoles with the enormous complex of endoplasmic reticulum, observed under the electron microscope, to my third cell type.

The microvilli cell possesses a strikingly dense and uniform array of microvilli. Below the luminal border many presumably pinocytotic vesicles occur abundantly dispersed throughout the apical half of the cell. Deeper in the cell there are much larger vacuoles which may merge and often contain large, osmiophilic granules.

FRETTER’s (1940) second cell type, which she describes briefly and generally, may be either my second cell type (the microvilli cell), or my third cell type with the concentric-layered vacuole bodies. TAYLOR’s (1968) description of his second cell type, together with his measurements of it, coincide with my observations of my second cell type. However, he calls these cells “lime cells,” a term I would rather reserve, following the literature cited below, for the designation of my third cell type.

Looking beyond *Elysia*, numerous other homologies exist within the opisthobranchs. Based on light microscopy, there are, for example, “cellules vacuolaires excrétrices” of HECHT (1895), “cellules vacuolaires” of ROUSSEAU (1935), and the “cells with excretion as main function” of BÜRGIN-WYSS (1961). SCHMEKEL & WECHSLER (1968), in one of the first studies of the digestive gland of an opisthobranch, *Trinchesia granosa*, based on electron microscopy, described the “D-Zelle” as possessing a profuse brush border and vacuoles with osmiophilic granules.

Schmekel & Wechsler considered excretion to be the main function of this cell type.

The literature of pulmonates, and indeed of all gastropods, provides many descriptions of cells similar to the microvilli cell. These can, however, be only briefly mentioned here. The first worker on the digestive gland of pulmonates, BARFUTH (1883), suggested that the "Fermentzelle" of *Arion* and *Helix* secretes enzymes. Later authors, for example THIELE (1953, on many pulmonates, several prosobranchs, and two opisthobranchs) and SUMNER (1965, on *Helix aspersa*) believed it to be excretory. WALKER (1970) came to similar conclusions in studying the digestive gland of *Agriolimax reticulatus*. His "excretory cell" closely corresponds in appearance to the microvilli cell of *Elysia*. I suggest that this cell takes up substances from the tubule lumen by pinocytosis and seals them in the vesicles, and that these vesicles then merge to form larger vacuoles until one large "telosomal" vacuole fills up nearly the entire cell. The presence of a profuse and dense brush border supports the hypothesis of a resorptive function in the microvilli cell. That the microvilli cell of *Elysia* releases the large vacuole into the lumen of the digestive gland for final excretion out of the body of the slug can as yet only be assumed. In *Trinchesia granosa* an exocytosis of the dark telosomal, "pigment" granules never takes place. Instead, they are accumulated until death (SCHMEKEL & WECHSLER, 1968).

The third cell type has not previously been described in *Elysia viridis*. Furthermore, only two cell types have been reported to date within the sacoglossans. In this respect, the sacoglossans differed from most of the other gastropods. My investigations show that a third cell type is present.

Cells of the third type lie displaced towards the base of the epithelium, rarely reaching the tubule lumen. In sections, they are triangular or rectangular in shape and are further characterized by the presence of round or oval vacuoles with typical concentric-structured contents. These vacuoles are surrounded by copious rough endoplasmic reticulum, which occasionally fills nearly the entire cell.

The "C-Zelle" of the aeolid *Trinchesia granosa* (SCHMEKEL & WECHSLER, 1968) corresponds nearly completely to the third cell type of *Elysia* in position, shape, extent of endoplasmic reticulum and finally in the presence of large vacuoles with diffuse, concentrically arranged, weakly osmiophilic content. The lime cells of the pulmonates show similar characteristics; ABOLINŠ-KROGIS (1961, 1965, 1970) on *Helix*, REYGROBELLET (1970) on *Limax*, and WALKER (1970) on *Agriolimax* reported cells with vacuoles containing concentric layers of alternating electron-dense and electron-translucent material. The illustrations in these studies look identical to those of *Elysia*. Therefore, the name "lime cell" should be reserved for this cell type, rather than as in TAYLOR (1968).

While ABOLINŠ-KROGIS (1961, 1965, 1970), as also BANI (1962) on *Vaginulus borellianus*, observed the central area to be filled with electron-dense material, WALKER (1970) could not establish this in *Agriolimax*. In the sections of

Elysia I frequently found spherical cores. ABOLINŠ-KROGIS (1965) believed that the "emptiness" of a vacuole could be a result of fixation and referred to the methods of BOOTHROYD (1964) for prevention of the decalcification of the vacuoles. ABOLINŠ-KROGIS (1961, 1965) described the "calcium spherites" of the "calcium cell" in *Helix* as consisting of an organic matrix in which inorganic salts are deposited. Later (1970), she described the origin and formation of the "calcium spherites." She regarded the different-looking but always concentrically structured vacuole bodies as different developmental stages. In my opinion, this also applies to the vacuole bodies of *Elysia*.

The function of the third cell type in most gastropods and in *Elysia* is still undetermined. In the early days, BARFUTH (1883) believed that the calcium was utilized in shell repair in *Helix*, and later workers, for example ABOLINŠ-KROGIS (1961, 1965), also put forward this theory. This function must be ruled out for the shell-less sacoglossan *Elysia*, and in most of my specimens cells of the third type were too well developed to be a relict of phylogenesis.

HIRSCH (1917) suggested that the spherules acted as a buffer reserve regulating the pH of the digestive tract in *Murex*, *Natica*, *Pterotrachea*, and *Pleurobranchaea*, and KRIJGSMAN (1928) shared this view for *Helix*. SCHMEKEL & WECHSLER (1968, on *Trinchesia granosa*) assumed secretion to be the general function of the vacuoles, which I accept for *Elysia*. Furthermore, I consider WALKER's (1970) proposition very interesting. He suggests that the lime cells act as a store of calcium which is utilized in mucus production as well as for the metabolism of the body in general. He referred to investigations proving that the mucus contains granules of calcium, which it is claimed make the mucus more viscous. This might well be one of its functions in *Elysia*: the tubules of the digestive gland occasionally seem to lie close to the mucous cells of the epidermis. Sometimes even the basal lamina of the ectoderm and of the endoderm seem contiguous and the haemolymph space becomes exceedingly narrow.

Further studies on this third type of cell will be necessary to determine its proper function. It may be, perhaps, that for each group it performs a different function.

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Behavioral Interactions Among Nudibranchs Inhabiting Colonies of the Hydroid *Obelia geniculata*

by

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Abstract. Behavioral interactions among four species of nudibranchs (*Dendronotus frondosus*, *Doto coronata*, *Eubbranchus exiguus*, and *Tergipes tergipes*) were studied to determine whether interference governs their distributions and feeding locations within colonies of the hydroid *Obelia geniculata*. Initial behaviors displayed by nudibranchs when approaching other nudibranchs were similar. Nudibranchs initiated contact by touching with the rhinophores or apparent “tasting” with the oral lobes. Encounters were brief, and the response of any nudibranch to contact varied, but was generally non-aggressive. Nudibranchs were not displaced from an area within a hydroid colony by heterospecific nudibranchs. The locations of *Tergipes*, *Dendronotus*, and *Doto* were affected by an increased density of conspecifics, but this pattern was inconsistent. Interspecific interactions between nudibranchs did not dictate where a nudibranch fed within the hydroid colony. In particular, the apparent lack of a limiting resource and the absence of aggressive interactions among individuals suggest that competition is unimportant in this community.

INTRODUCTION

Spatial dispersion and aggression have a great impact on the abundance and population dynamics of animals (BROWN & ORIAN, 1970; KING, 1973). Aggressive behavioral encounters among species in a community often determine the use of resources by those species. For example, in terrestrial communities aggression by stem boring insects (RATHCKE, 1976), dung beetles (BARTHOLOMEW & HEINRICH, 1978), and slugs (ROLLO & WELLINGTON, 1979) limits access to food resources and shelters of congeners and others. In those studies when individuals of different species interact, attacks by the superior individual resulted in injury or death of the subordinate. In other studies, interactions among species may be infrequent and occur only at high population densities. Experimental increases in densities of land snails depress activity and survival both of conspecifics and heterospecifics by interfering with feeding (SMALLRIDGE & KIRBY, 1988; BAUR & BAUR, 1990). Each of these cases describes interference competition, where the actions of individuals directly affect how other species use resources.

In marine intertidal habitats, aggressive encounters between gastropods restrict movements to particular areas of the shore. The Pacific mud snail *Cerithidea californica* (Haldeman) is confined to marsh pans in San Francisco Bay by behavioral avoidance of *Ilyanassa obsoleta* (Say) (RACE, 1982). In Barnstable Harbor, Massachusetts, the periwinkle *Littorina littorea* (L.) limits the microhabitat distribution of *I. obsoleta* in the mid-intertidal zone (BRECHLEY & CARLTON, 1983). *Littorina littorea* arouses *I. obsoleta* by grazing on its shell epiflora and this behavior interferes with the foraging, locomotory, and reproductive activities of the native snail. Aggressive interactions between limpets (*Patella* spp.) prevent access for home scars and territories on rocks (BRANCH, 1975, 1981). Although behavioral interactions among gastropods affect distributions in some systems, the phenomenon is not universal (WALDEN, 1981; CHOAT & ANDREW, 1986; BERMAN & CARLTON, 1991).

In marine epifaunal communities, hydroids provide food and habitat for many small, motile invertebrates, especially nudibranch mollusks (CLARK, 1975; LAMBERT, 1985). Nudibranchs either graze and crop polyps or penetrate the outer skeleton and suctorially remove the soft tissue (NYBAKKEN & McDONALD, 1981; LAMBERT, 1991a). The majority of nudibranchs within hydroid colonies are small (<5 mm), cryptic species. The abundance and presence of

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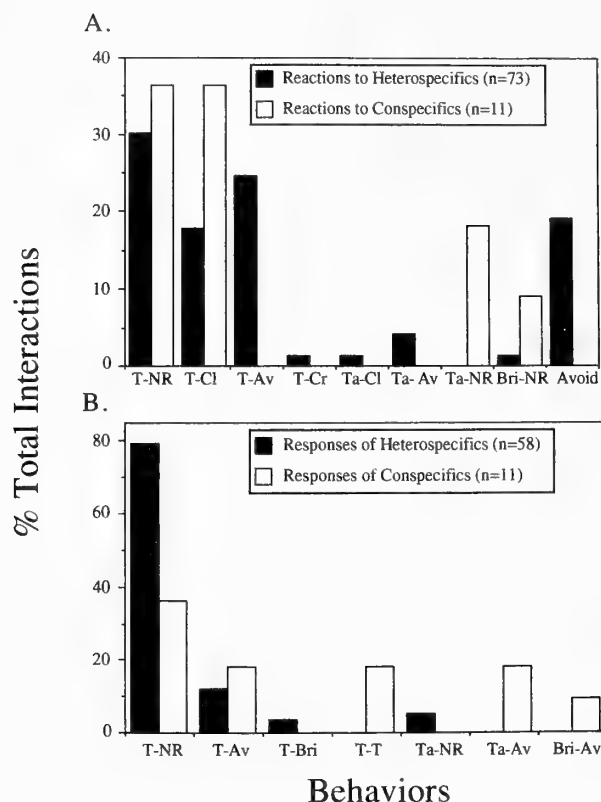


Figure 1

A. Behaviors of *Dendronotus frondosus* before and after initiating an encounter with other nudibranchs on colonies of *Obelia geniculata*. B. The responses of other nudibranchs to interactions with *D. frondosus*. (T = touch, Ta = taste, Cl = climb, Bri = bristle cerata, Cr = cringe, Av = avoid/aversion, NR = no reaction)

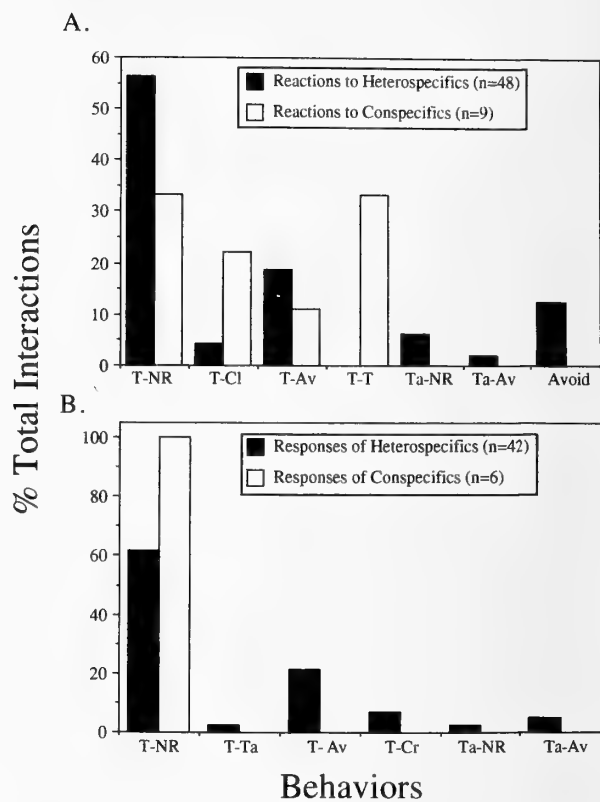


Figure 2

A. Behaviors of *Doto coronata* before and after initiating an encounter with other nudibranchs on colonies of *Obelia geniculata*. B. The responses of other nudibranchs to interactions with *D. coronata*. (T = touch, Ta = taste, Cl = climb, Cr = cringe, Av = avoid/aversion, NR = no reaction)

particular species of nudibranchs are often unpredictable, but when multiple species are present competition for food and habitat space seems likely.

In the southern Gulf of Maine, blades and stipes of the kelps *Laminaria saccharina* (L.) Lamour. and *L. digitata* (Huds.) Lamour. are often covered by the campanularid hydroid *Obelia geniculata* (L.). At least four species of nudibranchs are frequent predators and inhabitants of colonies of *Obelia* spp. in northern New England: *Dendronotus frondosus* (Ascanius, 1774), *Doto coronata* (Gmelin, 1791), *Eubranchius exiguus* (Alder & Hancock, 1848), and *Terigipes tergipes* (Forsk., 1775) (SWENNEN, 1961; CLARK, 1975; TODD, 1981; LAMBERT, 1991b). Encounters among these nudibranchs occur frequently, but the extent to which such interactions dictate how each species uses the hydroid colony is unknown. The present study assesses the behavioral interactions among the nudibranchs. The potential for interference to determine nudibranch distributions and feeding locations within the hydroid colony is discussed with respect to possible mechanisms of the species' coexistence in the community.

MATERIALS AND METHODS

Nudibranchs and hydroids were collected from a shallow (4–10 m), subtidal kelp bed at Cape Neddick, York, Maine, USA (43°10'N, 70°36'W) during May–September, 1989 (water temperatures: 10–18°C). Kelp blades were removed from stipes and placed in plastic bags while underwater. In the laboratory, nudibranchs were isolated by species and kept in mesh containers in flowing seawater tanks. Hydroid colonies were also kept in flowing seawater tanks until needed.

Behavioral Interactions

Nudibranchs were placed on portions of kelp blades covered with *Obelia geniculata* in 10-cm-diameter stacking dishes. Interactions between nudibranchs were observed with a stereo microscope and recorded. Behaviors were categorized into the following patterns (after ALLMON & SEBENS, 1988): (1) touch (contact of oral tentacles or rhinophores with the other nudibranch), (2) "taste" (contact of mouth with another nudibranch), (3) climb (movement of a nudibranch over or onto the back of another nudibranch),

(4) cringe (quick, muscular contraction of a nudibranch's body), (5) aversion or avoidance (movement away from another nudibranch), (6) bristle (the erection or movement of cerata toward another nudibranch), and (7) no reaction (NR) (either only the temporary retraction of rhinophores or no apparent movement).

Displacement and Nearest Neighbor

Pair-wise manipulative experiments tested whether the location of a nudibranch within a colony differed when among conspecifics or heterospecifics. Nudibranch densities in each treatment were consistent with field densities. The densities used for each species pair were, for *Tergipes* : *Dendronotus* (7:1), *Tergipes* : *Doto* (8:1), *Dendronotus* : *Doto* (6:1), and *Doto* : *Eubranchus* (2:3). Two combinations of species—*Tergipes* : *Eubranchus* (8:1) and *Dendronotus* : *Eubranchus* (5:1)—were not tested due to their unavailability.

Interspecific treatments were performed by separately placing nudibranchs of two species (A, B) onto three microscope slides with pieces of *Obelia*-covered kelp attached. Species A was introduced to the slides and allowed 24 hr to become established. Slides were suspended in open slide trays in an aquarium at ambient seawater temperature. After 24 hr the location of each nudibranch was documented. Four parameters identified the location of each nudibranch: height on an upright, density of hydrocauli in a 1 cm² area around the nudibranch, the distance between any two nearest nudibranchs (nearest neighbor), and the identity of the nearest neighbor. Hydrocaulus density was quantified to characterize the horizontal area of the colony occupied by a nudibranch. After the locations of individuals of species A were recorded, species B was introduced to the hydroid colony and the slides were re-suspended in aquaria for 24 hr. The removal and replacement of slides did not appear to disturb the nudibranchs; they were not dislodged from the hydroid colony. The location of each nudibranch was then again documented. A reciprocal pair-wise treatment was run simultaneously, allowing species B to establish first. To control for intraspecific interactions, monospecific treatments were conducted. Protocols were identical to heterospecific treatments and were run simultaneously.

Analysis of variance was utilized in a randomized block design (ZAR, 1984) to determine whether the location of a nudibranch differed when among conspecifics and heterospecifics. The pattern of spatial dispersion of individuals of each species of nudibranch was determined at both field densities and following an increase above field densities using nearest neighbor methods (CLARK & EVANS, 1954).

RESULTS

Behavioral Interactions

When approaching another nudibranch, the initial behaviors displayed by individuals of each species were sim-

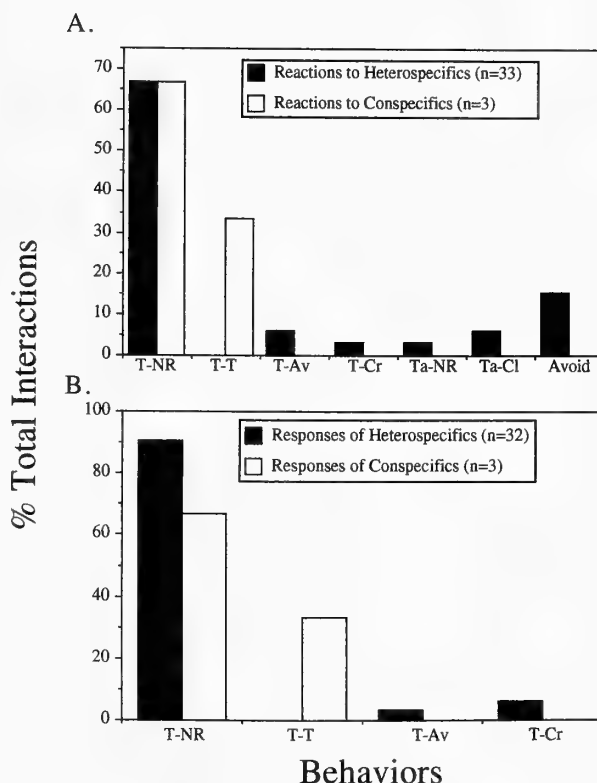


Figure 3

A. Behaviors of *Eubranchus exiguus* before and after initiating an encounter with other nudibranchs on colonies of *Obelia geniculata*. B. The responses of other nudibranchs to interactions with *E. exiguus*. (T = touch, Ta = taste, Cl = climb, Cr = cringe, Av = avoid/aversion, NR = no reaction)

ilar (Figures 1–4). Encounters usually occurred while one nudibranch was crawling across the kelp surface, whereas meetings between any two nudibranchs on a hydrocaulus were infrequent. On almost all occasions contact between heterospecifics involved the rhinophores or oral tentacles (Touch) or the mouth (Taste). These behaviors were non-aggressive and seemingly exploratory. Encounters were brief and the response of any nudibranch to contact varied, but both the initiator and the recipient generally reacted non-aggressively (62.1% and 81.4%, respectively). Actual aggressive behaviors and responses (bristling cerata or cringing) were infrequent and movements of an avoiding nudibranch were not different from the actions of a nudibranch climbing over another. The individual behavioral patterns for each species of nudibranch are described below.

Dendronotus frondosus

Dendronotus frondosus crawled across the kelp surface and among hydrocauli almost continuously; individuals were sedentary only when feeding. When *D. frondosus* approached another nudibranch any encounter was ini-

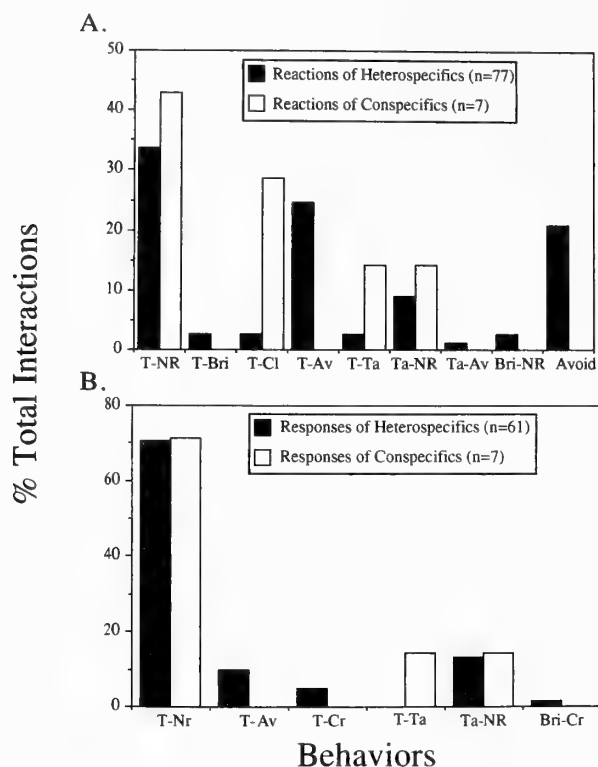


Figure 4

A. Behaviors of *Tergipes tergipes* before and after initiating an encounter with other nudibranchs on colonies of *Obelia geniculata*. B. The responses of other nudibranchs to interactions with *T. tergipes*. (T = touch, Ta = taste, Cl = climb, Bri = bristle cerata, Cr = cringe, Av = avoid/aversion, NR = no reaction)

tiated by contact with the oral tentacles or rhinophores, regardless of species (Figure 1). Following contact with another nudibranch, *D. frondosus* usually retracted its rhinophores, resulting in a "no reaction" response, or climbed over the other nudibranch (i.e., continued moving in the same direction) (Figure 1A). These responses to initial contact were, however, inconsistent. In 25% of the encounters with heterospecifics, *D. frondosus* turned away (Aversion) after initiating an encounter, and in 19% of the encounters *D. frondosus* turned away before any contact was made. These latter interactions occurred when *D. frondosus* was within close proximity (2–3 mm) of the other nudibranch.

The responses of nudibranchs to advances by *Dendronotus frondosus* were usually non-aggressive (Figure 1B). Most reactions involved simply a retraction of the oral tentacles or rhinophores by all species (NR). Heterospecifics were seldom displaced by *D. frondosus*, but conspecifics turned away in 46% of encounters.

Doto coronata

Individuals of *Doto coronata* were sedentary. It was common for any individual to remain atop a stolon for 2–3 hr during any observational period. Encounters initiated by

D. coronata were very similar and *D. coronata* touched the other nudibranch in 82.5% of encounters (Figure 2). Most often (67%) *D. coronata* followed contact behavior by retracting its rhinophores (NR) or by climbing (11%) over the other nudibranch (Figure 2A). *Doto coronata* occasionally retreated from encounters. Aversion behavior, as previously described for *Dendronotus frondosus*, occurred in 13% of encounters.

Reactions of heterospecifics to an encounter initiated by *Doto coronata* were variable (Figure 2B). Although nudibranchs most frequently did not react (64%), they did turn away in approximately 25% of interactions with *D. coronata*. The immediate behavior of conspecifics to *D. coronata* was one of no reaction (Figure 2B), and often the two nudibranchs then proceeded to copulate.

Eubranchus exiguus

When *Eubranchus exiguus* approached another nudibranch it initiated contact by touching (77%) or tasting (11%) and subsequently did not respond in 70% of these encounters (Figure 3A). *Eubranchus exiguus* avoided contact in 15% of all possible encounters. Reactions of *E. exiguus* to conspecifics were similar to the above pattern, and were not aggressive (Figure 3A).

Heterospecific nudibranchs did not respond to advances by *Eubranchus exiguus* in 91% of all encounters (Figure 3B). These nudibranchs appeared undisturbed and at most only retracted their rhinophores. Reactions of conspecifics to *E. exiguus* were non-aggressive; nudibranchs either did not respond (66%) or touched *E. exiguus* with the oral tentacles (33%) (Figure 3B).

Tergipes tergipes

Individuals of *Tergipes tergipes* were active; they crawled continuously across the kelp surface and up and down hydrocauli, stopping only briefly to feed on an exposed polyp. Most encounters initiated by *T. tergipes* were by either touching another nudibranch with the oral tentacles and rhinophores (68%) or tasting (11%) (Figure 4A). An aggressive behavior (bristling cerata at a heterospecific) was elicited very infrequently (3%). In cases where a response was elicited, *T. tergipes* reacted to encounters with other nudibranchs by retracting its rhinophores (NR) (45%). *Tergipes tergipes* turned away before meeting another nudibranch in 21% of cases and turned away after it initiated an interaction in 26% of encounters. Intraspecific encounters resulted in non-aggressive reactions by *T. tergipes* in all interactions (Figure 4A).

The majority of reactions of heterospecifics to *Tergipes tergipes* was retraction of rhinophores (NR) (84%) (Figure 4B). Conspecifics never reacted aggressively to an approach by another nudibranch.

Displacement Experiment

The overall area utilized by a nudibranch within a hydroid colony was generally not affected by additions of

Table 1

Location of nudibranchs in pair-wise manipulative experiments before and after an increase in nudibranch densities. Values are means (\pm SE) of nudibranch height (mm) on hydrocauli and density (number/cm²) of hydrocauli around a nudibranch. Treatment designations (A, B) refer to the identity and order of introduction of nudibranch species. (d.f. = degrees of freedom; NS = not significant.)

Treatment	Height				Density			
	d.f.	Before	After	P	d.f.	Before	After	P
<i>Tergipes : Dendronotus</i>								
AA	1,33	6.1 (± 1.0)	5.4 (± 1.1)	NS	1,33	9.3 (± 0.6)	6.4 (± 0.4)	0.001
AB	1,23	7.2 (± 1.6)	8.4 (± 1.5)	NS	1,23	10.1 (± 0.8)	8.7 (± 0.7)	NS
BA	1,4	0.0	0.0	NS	1,4	9.0 (± 0.6)	9.0 (± 0.6)	NS
BB	1,17	0.0	0.2 (± 0.2)	NS	1,17	9.7 (± 1.5)	6.2 (± 0.3)	0.002
<i>Dendronotus : Doto</i>								
AA	1,34	1.7 (± 0.9)	2.1 (± 0.8)	NS	1,34	6.5 (± 0.4)	6.3 (± 0.5)	NS
AB	1,27	2.6 (± 1.3)	2.3 (± 1.1)	NS	1,27	6.2 (± 0.5)	5.7 (± 0.4)	NS
BA	1,16	0.0	0.0	NS	1,16	6.7 (± 0.3)	6.0 (± 1.2)	NS
BB	1,23	0.0	0.4 (± 0.3)	NS	1,23	6.3 (± 1.5)	4.4 (± 0.2)	0.010
<i>Tergipes : Doto</i>								
AA	1,26	5.3 (± 2.1)	6.8 (± 1.1)	NS	1,41	6.1 (± 0.3)	5.0 (± 0.3)	NS
AB	1,37	4.3 (± 0.7)	6.9 (± 1.2)	NS	1,36	6.3 (± 0.4)	5.6 (± 0.5)	NS
BA	1,22	0.0	2.9 (± 2.9)	NS	1,22	6.3 (± 0.9)	4.7 (± 1.2)	NS
BB	1,23	0.0	0.7 (± 0.5)	NS	1,23	5.7 (± 0.3)	7.0 (± 0.6)	NS
<i>Doto : Eubranchus</i>								
AA	1,19	1.3 (± 1.3)	0.0	NS	1,19	4.8 (± 1.0)	7.2 (± 0.5)	0.030
AB	1,14	4.9 (± 3.5)	1.2 (± 1.2)	NS	1,14	5.3 (± 1.0)	7.4 (± 1.1)	NS
BA	1,8	7.8 (± 3.1)	4.8 (± 0.8)	NS	1,8	6.4 (± 0.8)	6.7 (± 0.7)	NS
BB	1,11	3.0 (± 1.3)	0.5 (± 0.5)	NS	1,11	6.1 (± 0.5)	5.2 (± 0.7)	NS

heterospecifics or conspecifics. Positional height within the colony did not vary significantly in any of the four treatments (Table 1).

The area occupied by a nudibranch changed with respect to the density of hydrocauli in intraspecific trials only (Table 1). Nudibranchs generally moved to areas of the colony where the density of hydrocauli was less. The pattern of change was inconsistent among treatments for *Dendronotus frondosus* and *Doto coronata*. *Dendronotus frondosus* moved to an area of fewer hydrocauli in one treatment, but remained in an area with similar density in the other. *Doto coronata* moved to areas of higher and lower density and also remained among hydrocauli of similar densities,

after an addition of nudibranchs. There was no change in the density of hydrocauli around *Eubranchus exiguus* after an addition of nudibranchs. *Tergipes tergipes* moved to areas with fewer hydrocauli after conspecifics were added to the hydroid colonies (Table 1).

Individual spacing between conspecifics did not vary among treatments (Table 2). Individuals of *Dendronotus frondosus*, *Doto coronata*, and *Tergipes tergipes* maintained a similar distance from conspecifics regardless of the identity of the other nudibranch species present. Within each treatment involving these three species, inter- and intra-specific distances were similar for each of the species of nudibranch (Table 2, Treatment 1, 2, 3). Spacing between

Table 2

Summary of patterns of spacing in interspecific associations of nudibranchs on colonies of *Obelia geniculata*. Values are mean distances (mm) between any two nearest neighbors. (* Distances between individuals from monospecific trials.)

Treatment	Species A	Species B	Distance (mm) between individuals (\pm SE)	n	P
1.	<i>Tergipes</i>	<i>Tergipes</i>	14.2 (\pm 2.2)	22	NS
	<i>Tergipes</i>	<i>Dendronotus</i>	16.2 (\pm 4.0)	11	
	* <i>Dendronotus</i>	<i>Dendronotus</i>	10.2 (\pm 1.8)	16	
2.	<i>Tergipes</i>	<i>Tergipes</i>	10.5 (\pm 1.1)	40	NS
	<i>Tergipes</i>	<i>Doto</i>	11.8 (\pm 4.0)	13	
	* <i>Doto</i>	<i>Doto</i>	6.7 (\pm 1.9)	22	
3.	<i>Dendronotus</i>	<i>Dendronotus</i>	11.7 (\pm 1.6)	27	NS
	<i>Dendronotus</i>	<i>Doto</i>	11.2 (\pm 1.2)	8	
	* <i>Doto</i>	<i>Doto</i>	7.8 (\pm 1.7)	22	
4.	a. <i>Doto</i>	<i>Doto</i>	6.4 (\pm 2.9)	6	a:b 0.027 b:c NS
	b. <i>Doto</i>	<i>Eubranchus</i>	15.1 (\pm 2.1)	13	
	c. <i>Eubranchus</i>	<i>Eubranchus</i>	21.0 (\pm 3.7)	8	

individuals of *Doto coronata* and *Eubranchus exiguus* differed (Table 2, Treatment 4). Individuals of *Doto coronata* were closer to each other than to *E. exiguus*, but distances between individuals of *E. exiguus* did not differ from interspecific distances with *Doto coronata*.

Nearest neighbor analysis (CLARK & EVANS, 1954) was used to determine the pattern of dispersion among conspecifics for the four species of nudibranchs. At average field densities, *Dendronotus frondosus* and *Tergipes tergipes* were distributed regularly, and *Doto coronata* and *Eubranchus exiguus* were randomly distributed throughout the hydroid colony (Table 3). The pattern of dispersion changed only when densities of *Doto coronata* were increased; *Doto coronata* tended to aggregate (clump) at higher densities. Patterns of dispersion did not change when densities of *Doto frondosus*, *E. exiguus* and *T. tergipes* were increased.

DISCUSSION

Behavioral encounters between any two nudibranchs occurred frequently, but aggressive encounters were rare and interactions did not influence the microhabitat utilized or the location where a nudibranch fed. Individual spacing between conspecifics was not generally altered at increased densities. ZACK (1976) described the behavioral patterns during encounters between pairs of *Hermisenda crassicornis* (Eschscholtz, 1831). The vast majority of these behavioral encounters were non-aggressive and involved two animals making contact, touching briefly, and withdrawing. He found no evidence of aggression or territoriality in field populations, although he hypothesized that agonistic behaviors serve to distribute animals over the substrate or to ensure access to food. Also, *Facelina bostoniensis* (Couthouy) feeds upon other nudibranchs and possibly conspecifics (personal observations; Todd, personal communication). Although these aggressive interactions may

disperse nudibranchs throughout a hydroid colony and possibly reduce competition, this is not apparent for the nudibranchs in *Obelia geniculata*.

Many ecological patterns are attributed to competition, but alternative hypotheses should be explored and assessed (LAWTON & STRONG, 1981). Interspecific competition has been designated the cause of niche separation, character displacement, and density compensation (SCHOENER, 1982; CODY & DIAMOND, 1975). However, despite the apparent lack of competition for food, the feeding behaviors of these four Gulf of Maine nudibranchs differ (LAMBERT, 1991a). LAWTON & STRONG (1981) stress that the important question to ask is not whether differences exist between species, but are the differences greater than other factors dictate?

A primary reason for rejecting interspecific competition as a major structuring force in this instance is the lack of intraspecific competition (MILLER, 1967; MORSE, 1980; STRONG *et al.*, 1984; KEDDY, 1989). Behavioral interactions between conspecifics were primarily non-aggressive (81%) (Figures 1–4) and at times resulted in the two nudibranchs mating.

Displacement from a feeding position was not observed and the dispersion of nudibranchs within the hydroid colony was altered by increased densities of conspecifics for one species; in this instance individuals aggregated. Two hypotheses are suggested to account for these observations. First, food resources are not limiting. Many researchers have inferred that nudibranchs exert ecologically important impacts on fouling communities by consuming particular hydroid prey (CLARK, 1975; HARRIS, 1987; TODD & HAVENHAND, 1989), but no work has yet experimentally demonstrated that food is limiting to these nudibranchs. Although CLARK (1975) shows an inverse relationship between egg production and predation index for *Catrina aurantia* (Winckworth) on colonies of *Tubularia* spp. that

Table 3

Patterns of intraspecific dispersion of nudibranch species on colonies of *Obelia geniculata*. Designations of "before" and "after" refer to an addition of individuals to manipulate densities of nudibranchs in pair-wise experiments. Patterns of dispersion (R) were determined by methods described in CLARK & EVANS (1954). (R = the degree the observed distance departs from a random expectation ($R = 1$).)

Species	n	Mean distance (mm) between individuals (\pm SE)			Pattern of dispersion			
		Before	n	After	Before		After	
					R	P	R	P
<i>Dendronotus</i>	6	13.3 (± 1.8)	7	13.0 (± 2.1)	1.48 (regular)	0.04	1.56 (regular)	0.02
<i>Doto</i>	2	11.2 (± 1.5)	5	2.5 (± 0.9)	0.72 (random)	NS	0.25 (clumped)	0.02
<i>Eubranchus</i>	3	12.2 (± 4.9)	5	10.4 (± 0.4)	0.96 (random)	NS	1.05 (random)	NS
<i>Tergipes</i>	7	14.1 (± 1.9)	8	13.3 (± 1.8)	1.69 (regular)	0.01	1.71 (regular)	0.004

suggests fecundity decreases when nudibranchs are present at high densities, most hydroid-eating nudibranchs are opportunistic, fugitive species with short life-spans and a single reproductive period just prior to death (TODD, 1981, 1983). Thus by the time a hydroid colony is eliminated, nudibranchs within the colony may well have concluded reproduction and begun to undergo senescence. Second, nudibranchs within the hydroid colony are generally indifferent to each other's presence. Nudibranchs contacted each other only while crawling within hydroid colonies. The majority of these interactions was non-aggressive and recognition of other nudibranchs by a mechanism other than tactile contact was rare.

Variable recruitment may function to regulate communities and reduce competition (CREESE & UNDERWOOD, 1982; QUINN & RYAN, 1989). Although these four nudibranchs have similar recruitment patterns (LAMBERT, 1991b) with peaks in colonization occurring during the summer months when food is plentiful and alternative foods are available (personal observations; Kuzirian, unpublished data), their abundance patterns vary between years, suggesting non-equilibrium patterns of coexistence (LAMBERT, 1991b). *Obelia geniculata* also grows epiphytically on *Agarum cribrosum* (Mertens) Bory and there are other common thecate hydroids on rocky substrate (personal observations). These represent potential alternative habitats and food resources for settling veligers that would reduce competitive interactions and promote coexistence. Also, CLARK (1975) speculated that competent veligers of *Cratena pilata* (Gould) may discriminate among potential settling sites that are occupied by competitors to decrease interactions (see also, GROSBERG, 1982).

Predation by the wrasse *Tautoglabrus adspersus* (Walbaum), which is a visual, epibenthic predator, may regulate the nudibranch populations and also facilitate coexistence of the nudibranchs. The majority (82.6%) of nudibranchs inhabiting *Obelia geniculata* colonies are less than 3 mm

in length (LAMBERT, 1990). These animals are immature (SWENNEN, 1961; MILLER, 1962; ROBILLIARD, 1970) and apparently cryptic. It is likely that as nudibranchs grow they are more susceptible to fish predation by *T. adspersus* because this teleost readily eats nudibranchs both in the laboratory (HARRIS, 1986; unpublished data) and in the field (personal observations). Large nudibranchs are more likely to be encountered and eaten by fish non-specifically grazing the hydroid colonies.

Nudibranchs associated with *Obelia geniculata* have different radulae and feed by different mechanisms (LAMBERT, 1991a). Dietary specialization has been suggested to alleviate competition for a number of gastropod species (NYBAKKEN & EASTMAN, 1977; BLINN *et al.*, 1989; HAWKINS *et al.*, 1989; MAZZELLA & RUSSO, 1989). Also, shifting to other prey species can reduce competition by decreasing feeding pressure in the habitat where veligers are most likely to settle. *Dendronotus frondosus* exploits *O. geniculata* probably only as juveniles and feeds on the hydroids *Tubularia* spp. when larger (>10 mm) (SWENNEN, 1961). THOMPSON & BROWN (1984) and Kuzirian (unpublished data) state that *Doto coronata* feeds on other hydroids as adults. The majority of *Doto coronata* found on the hydroid *Thuiaria argentea* (L.) was greater than 3 mm over 4 years (1972–1975) (Kuzirian, unpublished data) whereas 71.3% of *Doto coronata* in *Obelia geniculata* was less than 3 mm (LAMBERT, 1990).

Selection of specific sites to live within a larger area may allow coexistence (BIRCH, 1979; FLETCHER & UNDERWOOD, 1987; MAZZELLA & RUSSO, 1989). Nudibranchs use different areas within *Obelia geniculata* colonies (LAMBERT, 1991a). *Dendronotus frondosus* is found throughout the colony on hydrocauli, but is present only when small (<5 mm). *Doto coronata* occupies the edges of the colony on the kelp surface. *Eubranchus exiguus* exists also at the edges of the colony, but mainly on hydrocauli. *Tergipes tergipes* is generally located in the center of *O.*

geniculata colonies atop the hydrocauli. Thus *T. tergipes* is further specialized in its use of the hydroid colony in occupying a third dimension; the other three nudibranchs are two-dimensional specialists.

A low diversity of nudibranch species is present in the northwest Atlantic compared to the northeastern Pacific and British Isles (MARCUS, 1961; FRANZ, 1970; TODD, 1981). CLARK (1975) suggested that "climatic stability" with respect to biogeographical patterns of species is the primary reason for the low diversity in the northwestern Atlantic because annual variation in the water temperatures may be $>20^{\circ}\text{C}$. He proposed that these climatic effects could influence the degree of competition and behavioral interactions among co-occurring nudibranchs. In southern New England CLARK (1975) recorded the co-occurrence of *Cratena pilata*, *Tergipes tergipes*, and *Tenellia fuscata* (Gould) on *Obelia geniculata* and suggested that rising water temperatures influence competition by eliminating a competitor from a community. Thus a temporal separation of nudibranch populations might occur via differences in thermal tolerance of the respective species.

GERHART (1986) suggested that colonial marine invertebrates and their gastropod predators have important parallels to terrestrial plant-herbivore communities. In each system the prey have a large capacity to regenerate lost parts, and consumers are partial predators (HARVELL, 1984) capable of sequestering components of the prey for their defense (EDMUNDS, 1966; RHOADES & CATES, 1976). The roles of nudibranchs in this hydroid community appear analogous to those of leaf-eating and tissue-sucking insects on plants. In particular, although differences in feeding structures and microhabitat selection could mediate community structure (HAJEK & DAHLSTEN, 1986; LAMBERT, 1991a), the apparent lack of a limiting resource and the absence of aggressive interactions among individuals (ROOT, 1973; ZACK, 1976; SIMBERLOFF, 1978; LAWTON, 1982; STRONG, 1982; this study) suggest that competition is unimportant in these communities (see review, STRONG *et al.*, 1984). Future considerations of this parallel may provide new insights and generalizations on the evolution of predator-prey systems.

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Redescription and Taxonomic Reappraisal of the Tropical Indo-Pacific Nudibranch *Siraius nucleola* (Pease, 1860) (Anthobranchia: Doridoidea: Dorididae)

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Abstract. *Siraius nucleola* (Pease, 1860) is widespread in the tropical Indo-Pacific Ocean. Material for this paper comes from coastal and oceanic (*i.e.*, Norfolk Island) Australian waters, where the species is common but previously unrecorded. A description of external and internal morphology is presented, not only for reconciling intraspecific variation in our material with that described in the literature, but also for separating generic and specific characters which are confused in previous accounts. Minor inconsistencies in body pigmentation, rhinophores, and gills not attributable to intraspecific variation are indicative of differing interpretations rather than of different species. *Doriorbis* Kay & Young is synonymized with *Siraius* Er. Marcus. As redefined on rhinophoral and radular characters, *Siraius* is enlarged to accommodate five species worldwide—*S. bicolor* (Bergh, 1884), *S. fretterae* (Thompson, 1980), *S. ilo* Er. Marcus, 1955, *S. kyolis* Ev. & Er. Marcus, 1967, and *S. nucleola* (Pease, 1860).

INTRODUCTION

The genus *Doriorbis* was erected by KAY & YOUNG (1969) for the small dorid nudibranch described by PEASE (1860) as *Doris nucleola*. The principal characters used by KAY & YOUNG (1969) to diagnose the genus were: simple pinnate gills forming a circle about the anus; gills retractile into a circular sheath; radular teeth simple except for the 6-8 "outer lateral" (*i.e.*, marginal) ones which bear small, apical (*i.e.*, pectinate) denticles; Y- or T-shaped, yellow, medial streak extending from the rhinophores to the mid-dorsum. We now recognize that these characters are a mixture of generic and specific ones, so there is a need to separate them for the benefit of future workers investigating taxonomy or phylogeny in the Dorididae.

Twenty-four specimens of *Siraius nucleola* have been recorded along the coast of Australia since 1959. Eight of

the 20 animals discovered in Queensland were collected for this study. Four were dissected and the remaining four, all from Statue Bay, Yeppoon, have been deposited intact in the Museum of Tropical Queensland (formerly Queensland Museum [North Queensland Branch]), Townsville, under the registration number MO17432. A further nine specimens were collected at Norfolk Island in the Tasman Sea off Australia's east coast during the course of this investigation.

TAXONOMY

Order Nudibranchia Blainville, 1814

Suborder Anthobranchia Férussac, 1819

Superfamily DORIDOIDEA Odhner, 1934

Family DORIDIDAE Rafinesque, 1815

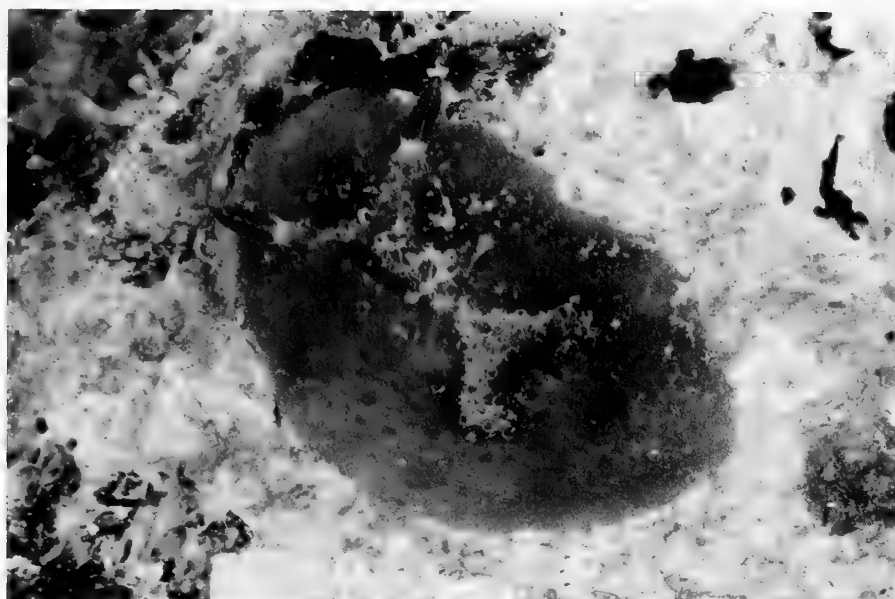


Figure 1

Siraius nucleola. Specimen photographed live; length 14 mm. From intertidal zone, Statue Bay, Yeppoon, central Queensland, Australia, 16 June 1988. Photograph: Jon Brodie.

Genus *Siraius* Er. Marcus, 1955

Siraius nucleola (Pease, 1860)

(Figures 1–17)

Synonymy

- Doris nucleola* PEASE, 1860:29, no. 31; ABRAHAM, 1877:211, *Doris* species 148; BERGH, 1881:pl. G, figs. 10, 11; PRUVOT-FOL, 1947:108.
Doris papillosa PEASE, 1860:30, no. 34; PRUVOT-FOL, 1947:108 (misidentification, not *Doris papillosa* Müller, 1776, or *Doris papillosa* Kelaart, 1858).
Doris tinctoria PEASE, 1864:510 (replacement name for *Doris papillosa* Pease, 1860).
Doris carinata ALDER & HANCOCK, 1864:122, pl. 29, figs 5, 6 (misidentification, not *Doris carinata* Quoy & Gaimard, 1832).
Doris carina ABRAHAM, 1877:209, *Doris* species 122 (replacement name for *Doris carinata* Alder & Hancock, 1864).
Doris papillata [sic = error pro *papillosa*] Pease: ABRAHAM, 1877:211, *Doris* species 147.
Platydorina immonda RISBEC, 1928:84, pl. 1, fig. 4, text fig. 12; RISBEC, 1953:30.
Doriorbis nucleola (Pease): YOUNG, 1969:423; KAY & YOUNG, 1969:178, 179; KAY, 1979:458, fig. 148A.
Halgerda rubicunda Baba: ORR, 1981:43 (misidentification, not *Halgerda rubicunda* Baba, 1949).

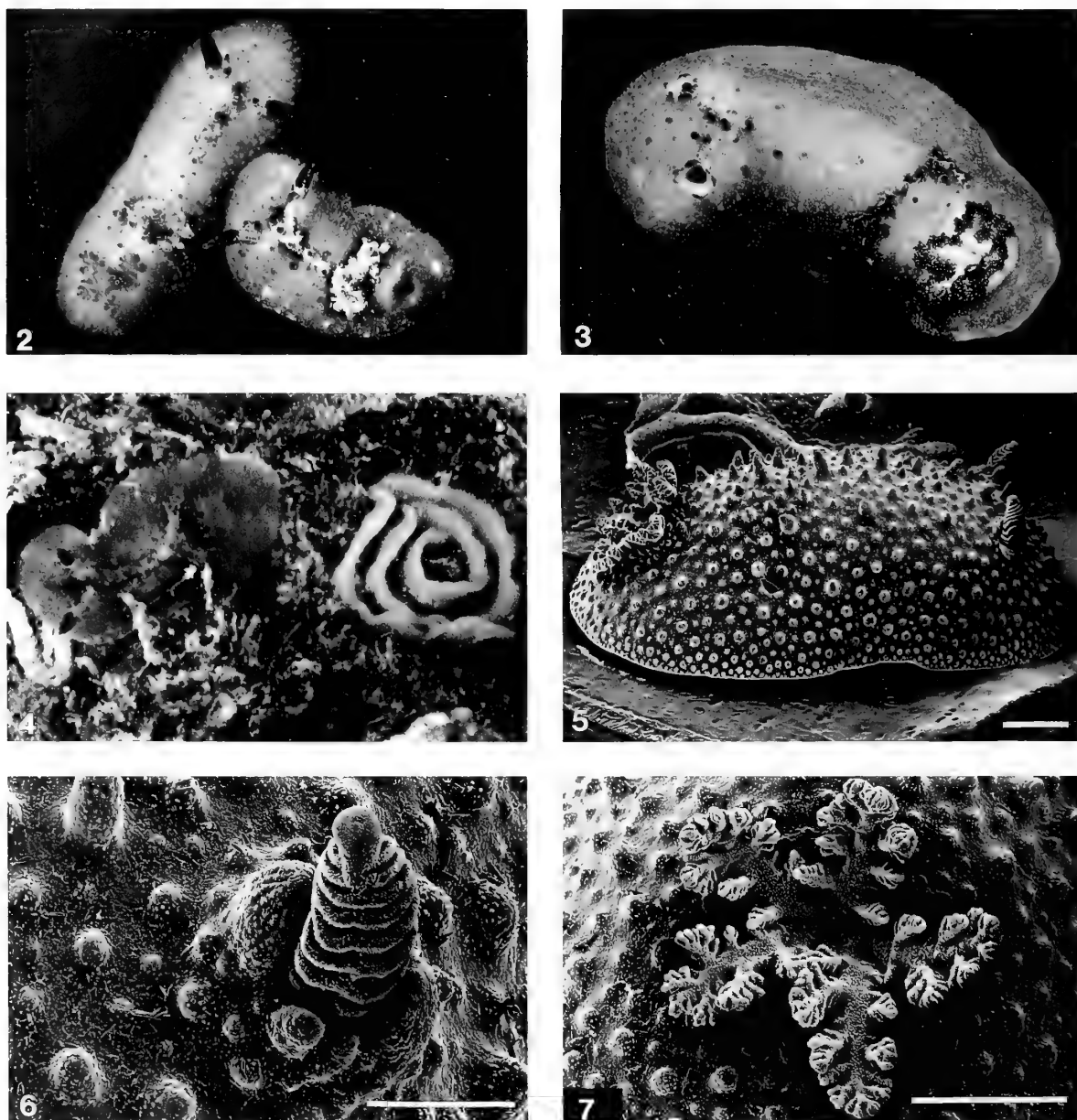
No complete synonymy has been presented before. KAY & YOUNG (1969) laid the foundations when they concluded the names *Doris nucleola* Pease, 1860, and *D. papillosa* Pease, 1860 (= *D. tinctoria* Pease, 1864) were synonymous and, acting as first revisers, selected *D. nucleola* as the name

for this species. At the same time they created the new generic name *Doriorbis*. ABRAHAM (1877) had realized much earlier that *D. carinata* Alder & Hancock, 1864, was preoccupied by *D. carinata* Quoy & Gaimard, 1832, but in creating the replacement name, *D. carina*, Abraham only added another junior synonym. RISBEC's (1928) name *Platydorina immonda* is a further synonym. We are confident of this from the description of body coloration and mantle ornamentation. RISBEC (1953:30) himself indicated that *P. immonda* might be the same as *D. carinata* Alder & Hancock.

References to this species since RISBEC (1953) have failed to present the entire synonymy (KAY & YOUNG, 1969; YOUNG, 1969; ORR, 1981), so we have done so for completeness.

Doris nucleola possesses no generic character that might exclude it from *Siraius*. As stated above, KAY & YOUNG (1969) created the genus *Doriorbis* solely for *D. nucleola* Pease and they did not mention *Siraius*. Had they been aware of that genus, they would almost certainly have opted to include *D. nucleola* in it. Actually, R. Burn recognized the synonymy of *Doriorbis* and *Siraius* some 15 years ago (Burn, personal communication, 1991).

Since *Siraius* is not a Latin or Greek word and ER. MARCUS (1955) gave no etymology, we take its gender to be masculine. Further, we interpret the specific name *nucleola*, which is derived from a Latin word meaning a "little nut" or "kernel," as a noun in apposition and accordingly its termination will not change to *-us* to agree with the gender of the genus. Therefore the correct combination is *Siraius nucleola*.



Explanation of Figures 2 to 7

Figures 2-7. External morphology of *Siraius nucleola*.

Figure 2. Lengths 13, 11 mm. From low tide, "The Strand," Cleveland Bay, Townsville, northern Queensland, 20 March 1989. Photograph: R. C. Willan.

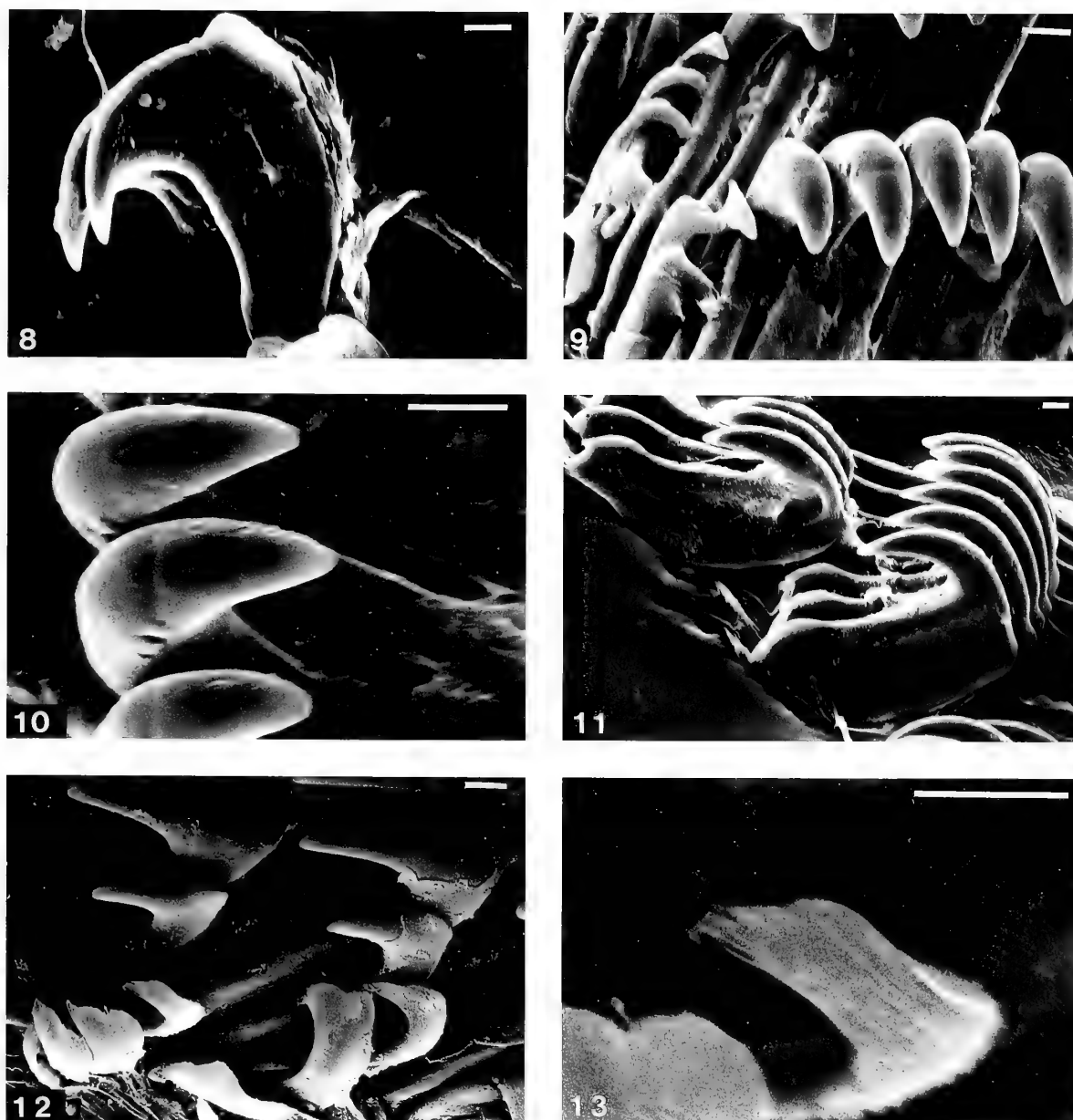
Figure 3. Length 21 mm. From 12 m, northern side of North West Solitary Island, northern New South Wales, 6 April 1991; note that rhinophores are retracted. Photograph: R. Gentle.

Figure 4. Length not recorded. From low tide, Statue Bay, Yeppoon, central Queensland, 16 June 1988. Spawn mass on right. Photograph: J. Brodie.

Figure 5. SEM of whole animal, length 12 mm. From low tide, "The Strand," Cleveland Bay, Townsville, northern Queensland, 8 March 1988. Bar = 1 mm.

Figure 6. SEM showing detail of right rhinophore and ornamentation on surrounding mantle of specimen depicted in Figure 5. Bar = 0.5 mm.

Figure 7. SEM showing detail of extended gills of specimen depicted in Figure 5. Bar = 1 mm.



Explanation of Figures 8 to 13

Figures 8–13. Radula of *Siraius nucleola*. Bar = 10 μ m in all figures.

Figure 8. SEM of inner face of two inner lateral teeth (approximately row 6, teeth numbers 5 and 6).

Figure 9. SEM of one row (number 20 approximately) of outer lateral teeth showing outer faces.

Figure 10. SEM of same row as in Figure 9 showing detail of outer faces of two outer lateral teeth; note denticles at base of cusp.

Figure 11. SEM of one row (number 30 approximately) of outer lateral teeth showing inner faces; note absence of denticles at base of cusp.

Figure 12. SEM of outermost lateral (above) and marginal teeth (below) of two rows (numbers 18 and 19 approximately) showing outer faces.

Figure 13. SEM showing detail of most marginal tooth; note apical fringe of minute denticles.

Material Examined

In the following list, locations on the Australian coast are given first. They are arranged counterclockwise starting with the southeasternmost one. The Norfolk Island localities then follow with the same arrangement. Measurements are those of animals in the extended crawling state.

AUSTRALIA: 1 specimen (21 mm), 12 m, northern side of North West Solitary Island, northern New South Wales (30°01'S, 153°16'E), B. Morgan, 6 April 1991 (color transparency only available for examination); 1 specimen (12.5 mm), intertidal, Angourie Pool, northern New South Wales (29°29'S, 153°21'E), R. Burn, 3 October 1959 (National Museum of Victoria, Reg. No. F27396); 11 specimens (2–14 mm), intertidal, Statue Bay, Yeppoon, Queensland (23°10'S, 150°47'E), G. & J. Brodie, 27 March 1988; 4 specimens, intertidal, Statue Bay, Yeppoon, Queensland (23°10'S, 150°47'E), J. Brodie, 22 May 1988; 2 specimens, intertidal, Statue Bay, Yeppoon, Queensland (23°10'S, 150°47'E), J. Brodie, 16 June 1988; 1 specimen, intertidal, Putney Beach, Great Keppel Island, Queensland (23°10'S, 150°58'E), J. Brodie, 10 April 1988; 2 specimens (13, 11 mm), intertidal, "The Strand," Cleveland Bay, Townsville, Queensland (19°15'S, 146°49'E), G. Brodie, 8 March 1989; 1 specimen, 4.5 m, Bundegi Reef, Exmouth Gulf, central Western Australia (21°51'S, 114°10'E), N. Coleman, 27 August 1972 (color transparency only available for examination).

NORFOLK ISLAND (29°01'S, 167°59'E): 1 specimen (7 mm), 11 m, Ball Bay, S.E. coast of Norfolk Island, D. & R. Gentle, November 1991; 1 specimen (11 mm), 6 m, "The Fireplace," Duncombe Bay, N.W. coast of Norfolk Island, D. & R. Gentle, November 1991; 1 specimen (13 mm), 12 m, offshore from "Crystal Pool," S.W. coast of Norfolk Island, K. Whysall & R. C. Willan, 16 March 1992; 1 specimen (3 mm) with bifurcated left rhinophore, 3 m, Slaughter Bay, S. coast of Norfolk Island, K. Whysall, February 1992; 2 specimens (10, 6 mm), 15 m, "Coral Garden," N.E. tip of Nepean Island, just south of Norfolk Island, D. & R. Gentle, November 1991; 1 specimen (11 mm), 15 m, Spin Bay, S.E. coast of Phillip Island, south of Norfolk Island, K. Whysall & R. C. Willan, 17 March 1992; 2 specimens (10, 10 mm), 14 m, Sail Rock, northern coast of Phillip Island, south of Norfolk Island, K. Whysall, November 1991.

Description

Maximum length is 21 mm, though 10–13 mm is more usual for adults. In life (Figures 1–4), the body of *Siraius nucleola* is elongate-ovate and flatly convex in profile. Although the mantle appears smooth at first glance, it actually possesses numerous, rounded pustules. The mantle, which covers the foot at all times, even posteriorly, is firm and feels rough because of a dense subepidermal layer of spicules. In addition to the pustules, a few taller papillae are present along the dorsal midline (Figure 5). Neither

body shape, nor the dimensions of the pustules/papillae are altered by preservation.

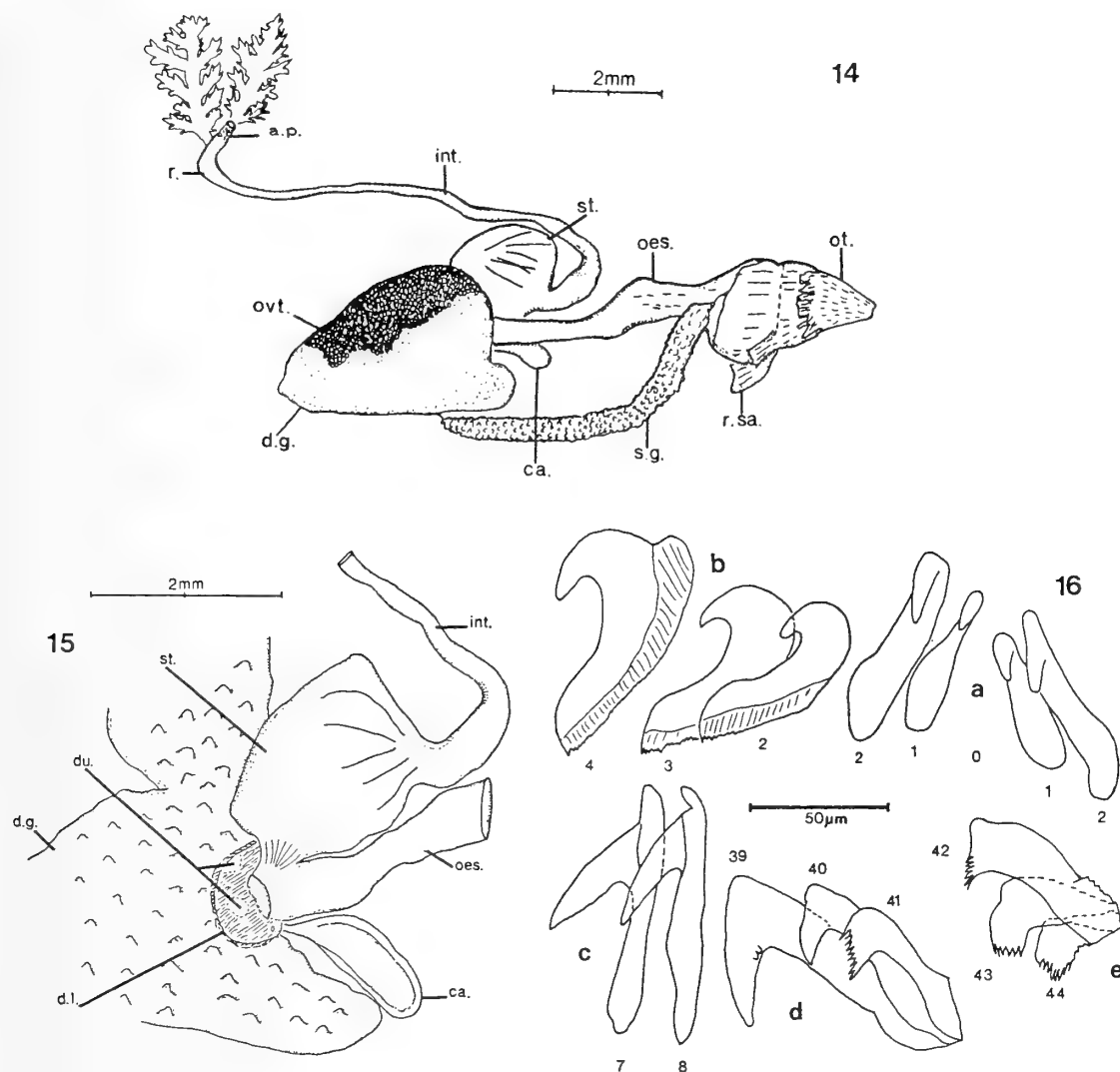
The rhinophores are relatively large and fully retractile. The clavus is elongate with widely spaced lamellae and a blunt apex. Both of the two specimens (14 and 10 mm) from Statue Bay, Queensland, had 10 lamellae on the right clavus. The rhinophoral pockets possess 5 to 7 upstanding papillae around their rim (Figure 6). These papillae are not all the same size; the 2 lateral ones are considerably larger than the rest.

The 5 gills, shown extended in Figure 7, are tripinnate.

The group of 11 specimens observed at Statue Bay on 27 March 1988 possessed either dull yellow-orange or dark tan or dark green mantles. Besides these colors, other specimens from Australia had khaki, orange, dirty yellow, or blue-black mantles. Every specimen had a dull orange-yellow mantle undersurface and foot sole. A sprinkling of granules imparted a brown coloration to the apices of the pustules on the mantle. A pale hourglass-shaped patch extended mid-dorsally from between the rhinophores to just in front of the gills. This patch can be interrupted or less pronounced in small specimens. It was opaque white or light brown, consistently paler than the mantle, and it sometimes had a narrow, purplish brown marginal zone. After preservation, the patch retained a faint violet hue. In all specimens, the rhinophores bore a cream base and dirty brown to black clavus which, like the dorsal patch, sometimes displayed a purplish tinge. The gills were uniformly brown, and consistently paler than the mantle.

The specimen from North West Solitary Island (Figure 3) was unusual in lacking the mid-central cream streak on the mantle, so that the transverse markings (the top and base of the "hourglass") behind the rhinophores and in front of the gills were disconnected. Its gills, which were broader than those possessed by other specimens, had opaque white bases and dark purple-brown extremities. Its gills and the mantle were peppered with numerous, microscopic, opaque white spots.

When the mantle is opened dorsally, the internal organs are clearly visible through the unpigmented walls of the thin, ensheathing visceral envelope. A composite view of the digestive system is given in Figure 14 and a more detailed view of the connections within the lumen of the digestive gland (*i.e.*, the openings to the oesophagus, caecum, and stomach) is given in Figure 15. The oral tube is relatively short and conical, and its junction with the pharyngeal bulb is marked by a circle of small extrinsic oral retractor muscles. A single, large extrinsic buccal retractor muscle is present on either side of the pharyngeal bulb ventrolaterally. A small radular sac lies beneath the expanded posterior half of the pharyngeal bulb. The paired salivary glands are tubular, flattened, and exceptionally long; each is connected to the posterior of the pharyngeal bulb by a narrow duct. These glands extend side by side beneath the oesophagus, the apex of each being tethered to the undersurface of the digestive gland by a thread of connective tissue. The oesophagus has a dilation just in



Explanation of Figures 14 to 16

Figures 14–16. Gut and radula of *Siraius nucleola*.

Figure 14. Composite view of structure of alimentary canal. Abbreviations: a.p., anal papilla; ca., caecum; d.g., digestive gland; int., intestine; oes., oesophagus; o.t., oral tube; r., rectum; r.sa., radular sac; s.g., salivary gland; st., stomach. Bar = 1 mm.

Figure 15. Detail of midgut; digestive gland partially removed to reveal interconnections of oesophagus, stomach, caecum, digestive gland, and intestine. Abbreviations: ca., caecum; d.g., digestive gland; d.l., cut wall of digestive gland; du., openings from digestive gland; int., intestine; oes., oesophagus; st., stomach. Bar = 1 mm.

Figure 16. Radula. a. Innermost lateral teeth, row 3, dorsal view. b. Inner lateral teeth, row 4, profile. c. Teeth 7 and 8, row 11. d. Outer lateral teeth, row 6, profile. e. Extreme outermost lateral teeth, row 6, profile.

front of its middle section. Dorsally, the cream-colored stomach was observed to be cupped between two anterior lobes of the digestive gland. A caecum opens into the lumen of the digestive gland below, and just to the left of, the common atrium of the oesophagus and stomach (*i.e.*, it is not encircled by the intestine). The intestine emerges from the stomach on the left side and disappears beneath it for a short distance before reappearing just to the right of the mid-dorsal line. It then passes over the top of the greenish

digestive gland (whose surface was covered by the cream ovotestis) and continues rearwards to end at the darkly pigmented anal papilla.

After treatment with potassium hydroxide, the pharyngeal bulb yielded a lightly cuticularized labial ring and a relatively broad yet elongate radula. There were definitely no jaws. Radulae of the 11- and 10-mm specimens from Statue Bay measured 1.2 and 1.1 mm long by 1.09 and 0.7 mm in maximum width, respectively, when spread out

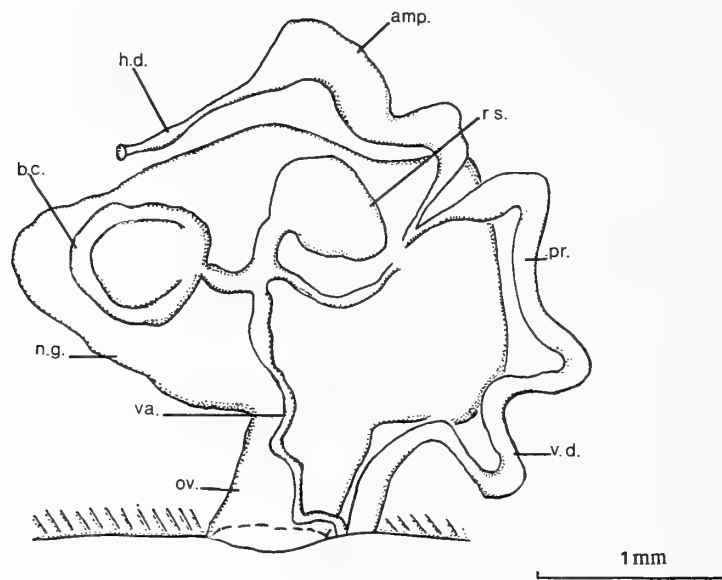


Figure 17

Siraius nucleola. Composite view of structure of reproductive organs of a sexually mature specimen. Abbreviations: amp., ampulla; b.c., bursa copulatrix; h.d., hermaphroditic duct; n.g., nidamental glands; ov., oviduct; pr., proximal section of vas deferens; r.s., receptaculum seminis; v.d., distal vas deferens.

and laid flat on microscope slides. Radular formulae were $34 \times 4.40.0.40.4$ (14 mm animal), $26 \times 3.34.0.34.3$ (11 mm animal) and $25 \times 3.26.0.26.3$ (10 mm animal).

Except for the outermost laterals and marginals, all the teeth are simple (*i.e.*, hamate) with flanges posteriorly. In the following account, numbers relate to individual teeth across one half-row near the growing end of the largest (14 mm) Queensland specimen. The innermost laterals (Figure 16a) are relatively small with a hooked cusp. Moving away from the midline, the laterals become larger and their cusps more erect (Figures 9, 16b, c). Nine of the outer laterals (tooth numbers 30–38) bear three minute denticles at the base of the cusp on the outer face (Figure 10). Outer lateral number 39 has two denticles (Figure 12) and outer lateral number 40 has none at all. The outermost three or four teeth (the marginals) bear an apical fringe of minute, pectinate denticles (Figures 12, 13, 16e).

A composite view of the unravelled reproductive system is presented in Figure 17. The hermaphrodite duct widens at about one-third its length into a shiny, white ampulla which is relatively elongate. The separation of the distal hermaphrodite duct into vas deferens and oviduct takes place within the nidamental gland mass. The vas deferens maintains its diameter throughout its length, the proximal (prostatic) section being tubular and not enlarged. Presumably the epithelium in this section is glandular, but this was not obvious on dissection and it was not checked histologically. No armature could be found on the exterior or interior of the simple penis. The vagina is long and narrower than the vas deferens with which it is contiguous

at the genital aperture. The bursa copulatrix and receptaculum seminis, both stalked, arise high up, side by side on the vagina (*i.e.*, semiserial arrangement). The bursa is spherical and thin walled. The receptaculum is slightly smaller than the bursa, ovoid, and thick walled.

Several egg masses were present alongside the specimens from Statue Bay (Figure 4) and these were identical to masses laid by captive animals. The masses were firm, gelatinous, orange spirals (2.5 to 3.5 whorls), and they had a slightly crenulate upper (*i.e.*, free) margin. The lower edge (*i.e.*, that attached to the substrate) of whorls was separated by gaps of 2 to 3 mm from adjacent whorls. There was only a single egg per capsule. The type of larval development and the mode of hatching were not recorded.

Comparison with Previous Descriptions

Although ALDER & HANCOCK (1864) provided no details of the internal anatomy of their *Doris carinata*, it is possible to recognize the species again positively because of the colored drawings executed by the Hindu artists commissioned by Walter Elliot (ALDER & HANCOCK, 1864: pl. 29, figs. 5, 6). The specimens depicted in their drawings, which are iconotypes because no actual animals were preserved, had olive green mantles with brown pustules and the hourglass-shaped patch on the mantle was pale with whitish pustules.

PEASE's (1860) specimens from Hawaii had orange (*Doris nucleola*) or grayish (*D. papillosa*) mantles. We have no doubt that our Australian specimens are conspecific with

those redescribed as *Doriorbis nucleola* (Pease) from Hawaii more than a century later (KAY & YOUNG, 1969). Kay & Young's photograph of a living animal reveals the gills to be tripinnate, thus contradicting their description of them as "simply pinnate." Other minor differences involve the number of papillae on the mantle surface (indicated as "a sparse scattering"), the size of the rhinophores (indicated as "small"), the blunt (rather than acuminate) apex to the rhinophores, and the color of the mid-dorsal hourglass-shaped patch (described as "a Y- or T-shaped yellow medial streak").

KAY & YOUNG's (1969) radular description is ambiguous in that it failed to discriminate between outer lateral and marginal teeth, and the mention of "small outer denticles" could relate to either the small basal denticles on the outer face of the outer laterals or the apical pectinations on the marginal teeth. However, because Kay & Young indicate there were 42 teeth across one half-row of the radula in their specimen and they illustrate the forty-second tooth in their figure 3, we interpret that tooth as the outermost marginal and hence the "small outer denticles" on it must be the apical pectinations. The corollary to this conclusion is that either the outer laterals were smooth or Kay & Young overlooked them on their specimen.

KAY & YOUNG's (1969) excellent diagram of the reproductive tract reveals an identical arrangement to that of our specimens, even to the connection of the hermaphrodite duct/vas deferens/oviduct within the nidamental gland mass. On no occasion have we observed the conglobating behavior (*i.e.*, rolling into a ball) mentioned by KAY & YOUNG (1969) as characteristic of *Doriorbis nucleola* when disturbed.

Discussion

ER. MARCUS (1955:134) defined *Siraius* on the basis of its simple lateral teeth, pectinate marginal teeth, short and grooved oral tentacles, short and broad salivary glands, tubular (as against enlarged) prostatic region of the proximal vas deferens, unarmed and protrusible distal vas deferens, lack of penial papilla, and semiserial arrangement of allosperm vesicles. He specifically excluded branchial and labial characters from his definition of *Siraius* because he believed they had no generic importance (ER. MARCUS, 1955:135). Later, EV. & ER. MARCUS (1967:66) dismissed the shape of the salivary glands as a generic character because of the apparent differences between the three species they had examined (ER. MARCUS, 1955; EV. & ER. MARCUS, 1967).

KAY & YOUNG (1969:178) singled out only three characters which they considered as "most important" for diagnosing *Doriorbis*: "(1) simply pinnate branchiae arranged as a circlet about a posterior, mid-dorsal anus and retractile into a circular sheath; (2) hamate lateral teeth with outermost laterals denticulate; (3) a Y- or T-shaped

yellow medial streak extending from the rhinophores to the mid-dorsum." Having re-examined the type species *Doriorbis nucleola*, we are now in a position to reappraise these three and other characters used to define *Doriorbis* and other related, jawless, caecate, cryptobranch dorids (*Doris*, *Etidoris*, *Siraius*, *Austrodoris*, *Alloiodoris*, *Artachaea*). The branchial form (which we call tripinnate) occurs in most other genera in this close-knit group, so it is not diagnostic. Nor, incidentally, are the character states of distal vas deferens, penis, and allosperm vesicles for the same reason. As clarified above, the radular configuration, especially the pectinate marginal teeth, is unique to only two genera within this group—*Siraius* and *Etidoris*. The color pattern is diagnostic of *S. nucleola* alone.

In our definition of *Siraius* (see below) we incorporate the state of the rhinophoral pocket (with papillae of unequal size around the margin) because that state occurs in four species—*Siraius bicolor*, *S. ilo*, *S. kyolis*, and *S. nucleola*.

Our redefinition of *Siraius* Er. Marcus (with autapomorphies and apomorphic traits in italics) is as follows. Small (to 30 mm crawling length), cryptobranch dorids with firm mantles supported by non-emergent spicules; mantle ornamented with low, scattered, spiculose tubercles (and sometimes papillae too); *rhinophoral pockets carrying papillae of unequal size around rims*; gills tripinnate; branchial pocket usually carrying papillae around rim; oral tentacles short and grooved; jaws absent; radula broad, lateral teeth simple, *marginal teeth pectinate*; stomach with caecum that rises to surface of digestive gland to left of intestine; vas deferens of uniform diameter, proximal (prostatic) section tubular and of uniform diameter, distal section protrusible—serving as penis and unarmed; bursa copulatrix and receptaculum semiserially arranged high up on vagina, of equivalent size, both stalked.

This redefinition of *Siraius* emphasizes rhinophoral and radular features because these are the only characters we interpret as derived (or apomorphic in cladistic terminology). Two taxonomically desirable outcomes stem from this redefinition. First, it enlarges *Siraius* to accommodate the western Atlantic *Doris fretterae* Thompson, 1980. The only discordant character possessed by that species is its smooth branchial pocket, but that state is primitive in the group under study and therefore it cannot be used to exclude the species from the genus. Table 1 compares the five species included in *Siraius* according to our definition. Second, it allows us to recognize *Etidoris* and *Doriopsis* as the sister genera to *Siraius*, because both also possess simple tubular prostatic sections of the proximal vas deferens. Most species in these three genera possess ribbonlike, flattened salivary glands (the exception being *S. ilo* Er. Marcus), equivalent-sized bursa copulatrix and receptaculum seminis, and close proximity of these two allosperm vesicles to each other on the narrow, straight vagina. The pectinate marginal teeth in *Siraius* and *Etidoris* indicate these two genera are closer to each other than either is to *Doriopsis*. This relationship is strengthened by the highly derived

Table 1
Comparison of morphological features of *Sirinus* species.

Species	Maximum (extended crawling) length (mm)	Mantle coloration	Rim to rhinophoral pocket	Gills	Salivary glands	Radular formula (maximum)	Outer lateral teeth	Habit	Location	Reference
<i>S. bicolor</i> (Bergh, 1884)	7	Translucent white; apertures of pustules yellow-brown	irregularly papillate; 2 lateral papillae largest	10; 3 or 4 anterior ones largest	long-ribbon-like	$33 \times 4.44-0.44.4$	smooth	intertidal	northern Mediterranean; Florida	ER. & EV. MARCUS, 1970
<i>S. fretterae</i> (Thompson, 1980)	30	Dark green; ventral surface bright orange	shown as irregularly papillate in illustration	9-11	?	$40 \times 3.40-0.40.3$	smooth	intertidal	Jamaica	THOMPSON, 1980
<i>S. ilo</i> Er. Marcus, 1955	25	Grayish-yellow with darker pustules in some individuals	pustules in part a ragged border	22	short, broad	$37 \times 3.44-0.44.3$	smooth	intertidal	Brazil; Trinidad	ER. MARCUS, 1955
<i>S. kyolis</i> Ev. & Er. Marcus, 1967	12	"Dirty yellow with blackish spots"; "tan with greenish-black spots"	4 lobed	11	ribbonlike; left reported as longer than right	$47 \times 2.35-0.35.2$	smooth	intertidal	Florida	EV. & ER. MARCUS, 1967
<i>S. nucleola</i> (Pease, 1860)	21	Generally orange, with pale "hourglass" streak between rhinophores and gills	5-7 papillae, 2 lateral ones largest	5	long, ribbonlike	$34 \times 4.40-0.40.4$	2 or 3 minute denticles at base of cusp on outer face	intertidal to 15 m	Indo-Pacific	KAY & YOUNG, 1969; present work

branchial configuration of *Doriopsis* wherein the gill circlet is compressed into a rearward-projecting fan overtopped by a notal flap.

Geographic Distribution

Siraius nucleola is now known from widely separated areas of the Pacific Ocean (Hawaii, New Caledonia, Hong Kong, Australia, Norfolk Island) and India. We assume that it ranges continuously throughout the tropical Indo-west Pacific region.

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Polygyrid Land Snails, *Vespericola* (Gastropoda: Pulmonata), 1. Species and Populations Formerly Referred to *Vespericola columbianus* (Lea) in California

by

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Abstract. *Vespericola columbianus pilosus* (Henderson, 1928) and *V. columbianus orius* (Berry, 1933) differ from typical Pacific Northwest *V. columbianus* (Lea, 1838) in shell and reproductive system characters and are separated as distinct species. A new species, *Vespericola marinensis*, is described and compared to *V. pilosus* and *V. columbianus*. Other California records based on shells of the *V. columbianus* type are summarized.

INTRODUCTION

This is the first in a projected series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. The greatest species diversity occurs in northwestern California and southwestern Oregon, where nine species have been named. One additional species is described herein. In addition, two species formerly regarded as subspecies of *Vespericola columbianus* (Lea, 1838) are shown to differ in genital characters from typical *V. columbianus* and are separated as distinct species. The material treated in this and following papers was collected by the authors from 1968 to 1991; additional material of many of the new taxa was located in museum collections. As remarked earlier (ROTH, 1985), the reproductive system in species of *Vespericola* is often more strongly differentiated than the shell. In many cases, shell characters are adequate for identification. However, especially in the complex of species resembling *Vespericola megasoma* (Pilsbry, 1928), dissection of the mature reproductive system is sometimes necessary for a firm identification. With specimens from new localities, it is always desirable to establish the species' identity by dissection.

Vespericola columbianus pilosus (Henderson, 1928), the type species of *Vespericola*, differs anatomically (and somewhat in shell characters) from *V. columbianus* from the valley of the Columbia River, Washington-Oregon, and

accordingly is separated as a distinct species. Its distribution, limited to central California, is reviewed. Populations in Marin County, differing in shell and anatomical characters from those on the San Francisco Peninsula, are described as a new species, *V. marinensis*. *Vespericola columbianus orius* (Berry, 1933) differs anatomically and conchologically from *V. columbianus* and is considered a separate species. Remaining Californian records based on shells of the *V. columbianus* type (i.e., those in which the inner part of the basal lip curves or angles forward in basal view and the inner lip is not markedly dilated over the umbilicus) are summarized as a basis for future investigation.

MATERIALS AND METHODS

Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of PILSBRY (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 30× magnification under a dissecting microscope with an ocular reticle. Three counts were taken per specimen and the mean (to the nearest integer) recorded.

Specimens for dissection were prepared by the method of MILLER (1967). Snails were first drowned in water to

insure expansion and relaxation, then heated to a temperature of 60°C, at which time the bodies could be pulled easily from the shells and dissected. After the body cavity was opened, the position and maturity of the reproductive system were observed; then the whole reproductive system was removed, attached to a small patch of body wall around the external genital orifice. The penis was slit longitudinally to expose the verge and the pilasters and papillae on the wall of the penial chamber. The verge of at least one specimen of every species was completely excised for examination.

Whole mounts of genitalia were prepared by the method of MILLER (1967): stained with hematoxylin, dehydrated and cleared in successive baths of ethanol and toluene, and mounted on slides with Permout mounting medium. Organ measurements were taken from mounted specimens. Anatomical drawings were made by projecting the image of the whole mount on paper with an overhead projector.

Shell growth in Polygyridae is determinate and ends with, first, a constriction of the body whorl and then a turning outward and thickening of the lip. Reproductive maturity normally seems to follow a short time after the lip turns, but the presence of a turned lip does not guarantee a reproductively mature specimen. Therefore, at least a portion of each sample was kept alive in a terrarium for a period of weeks or months before dissection to ensure full development of the genital structures. Terraria consisted of redwood boxes with screened tops. A 3–6 cm layer of soil and leafmold from the collecting locality was added. Specimens were fed lettuce. There is no indication that growth of *Vespericola* in terraria under these conditions is in any way abnormal.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; UCM, University of Colorado Museum; USNM, United States National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Family POLYGYRIDAE Pilsbry, 1895

Vespericola Pilsbry, 1939

Vespericola PILSBRY, 1939:xvii; PILSBRY, 1940:892–894; ZILCH, 1960:586.

Type species: *Polygyra columbiana pilosa* Henderson, 1928 [= *Vespericola pilosus* (Henderson)], by original designation.

Polygyridae with shell small to medium-sized, globose to depressed-helicoid, narrowly umbilicate to imperforate. Periostracum smooth, matte-surfaced, or granulose, bearing sparse to densely set setae (or at least their scars). Base of last 0.2-turn of body whorl more or less compressed upward; strong constriction present behind lip. Parietal

lamella present or absent (sometimes variably present within a species). Lip turned outward and sometimes reflected. No lamellae present on outer or basal lips, but low basal callus sometimes present. Epiphallus internally ridged, markedly narrower than apex of penis, usually with swollen, sausage-shaped upper section, terminating in bound, vestigial epiphallic caecum at junction of epiphallus and vas deferens. No penial gland present. Penial retractor muscle inserted on epiphallus, distant from penis. Retentor muscle originating on epiphallus or branching from penial retractor near epiphallus, inserting on summit of well developed penial sheath. Upper part of penial chamber bearing V-shaped pilasters or diverging rows of papillae; or, entire wall of chamber covered with close-set papillae. Paired longitudinal pilasters absent. Smooth, conical, spoon-shaped, or needle-like verge extending forward from summit of the penial chamber, containing seminal duct, with terminal or subterminal pore, without terminal papillae. Much of penis inserted into everted spermathecal duct in copulation; basal penis slightly expanded into small clasping disk. Verge directed forward during copulation.

Spider webs, soil, and bits of plant debris often adhere among the setae, forming a dark crust; the resulting appearance of the shell is cryptic and may mimic a mammal dropping.

The principal species-level diagnostic features of the reproductive system are the length of the atrium; the shape and dimensions of the penial complex, including the verge; the shape and size of the spermatheca ("gametolytic gland," "bursa copulatrix") and its duct; and the presence or absence of a fleshy thickening at or near the base of the spermathecal duct.

EMBERTON (1988, *e.g.*) does not recognize an epiphallus (as distinct from the proximal part of the vas deferens) in Triodontopsinae. We follow the convention of PILSBRY (1940) and other authors in terming as epiphallus the portion of the seminal duct from the insertion of the epiphallic caecum ("flagellum") to the apex of the penis.

The noun *Vespericola* is of masculine gender, so adjectival species names often end in *-us*.

The genus ranges around the northeast Pacific rim from the Aleutian Islands to San Luis Obispo County, California.

The family-group name Polygyridae Pilsbry, 1895, is junior to Mesodontidae Tryon, 1866. A petition to validate the better-known name Polygyridae (EMBERTON, 1989) has been affirmed (ICZN, 1992).

Vespericola pilosus (Henderson, 1928)

(Figures 1–6)

Polygyra columbiana pilosa HENDERSON, 1928:143; PILSBRY, 1928:181–182, 185 (in part), figs. 10, 10a; HENDERSON, 1929:80 (in part; *non* Alaska and Pacific Northwest records, and probably *non* fig. 35); HENDERSON, 1936:255 (reference to California localities only).

Vespericola columbiana pilosa (Henderson): PILSBRY, 1939:



Explanation of Figures 1 to 3

Figures 1–3. *Vespericola pilosus* (Henderson). Shell, BR 1648, CALIFORNIA: San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon, B. Roth coll., 4 June 1989. Top, apertural, and basal views. Diameter 13.9 mm.

xvii; PILSBRY, 1940:896–898 (in part), figs. 513:10, 513:10a (non figs. 512C, 512D); INGRAM, 1946:92 (in part); INGRAM & LOTZ, 1950:25–26 (in part), pl. 5, figs. 5, 6; LA ROCQUE, 1953:309 (in part).

Vespericola pilosa (Henderson): BAKER, 1962:16.

Non *Vespericola columbiana pilosa* (Henderson): WEBB, 1970:75–77.

Non *Vespericola columbiana* var. *pilosa* (Henderson): EYERDAM, 1951:7.

Diagnosis: A medium-sized *Vespericola* with depressed-helicoid to conical, narrowly umbilicate shell, 5.5–6.3 whorls, 19–30 periostracal setae/mm², and usually no parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 0.87; verge 0.5–0.6 mm long, conical, ending in 0.1 mm opposing lips.

Description of shell: Shell medium-sized for the genus (diameter 12.3–15.5 mm) depressed-helicoid to conical, narrowly umbilicate, with 5.5–6.3 whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately impressed. Embryonic whorls 1.5–1.7, with prominent, rather coarse, radial wrinkling; wrinkles surmounted by smooth, hemispheric to radially elongate papillae. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae and irregular granulation with collabral trend. Periostracum bearing slender setae in gently descending rows; setae 19–30/mm², approximately 0.2–0.25 mm long on spire and shoulder of body whorl, erect or curving away from direction of coiling, broadened at base. Surface between setae sharply microscopically granulose on spire (smoother on body whorl) and finely radially wrinkled. Periphery broadly rounded. Base tumid, papillose where setae worn off; setae shorter than on spire, extending into umbilicus. Umbilicus contained about 14 times in diameter. Body whorl weakly to moderately deflected downward, constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of about 35° to shell axis. Lip turned outward and reflected, especially at base; basal lip sometimes with faint, elongate internal thickening. Parietal lamella usually absent (but present in the holotype and in San Francisco Presidio population). Inner part of basal lip straight or gently curved

forward, moderately dilated, covering about half of umbilicus. Periostracum warm brown; lip pinkish buff.

Description of soft anatomy: Eight specimens from San Bruno Mountain (regarded as virtual topotypes for the reasons discussed below) were dissected.

Color of living animals tan to brown, darker and grayer on body-stalk. Mantle over lung 10–50% maculated with black.

Atrium (Figure 4) of moderate length for genus. Penis elongate-conical, with anterior, basal portion enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of penial chamber bearing papillose pilasters in diverging V-pattern (Figure 5). Slender peduncular section of about 2.0 mm present between base of sheath and junction with atrium.

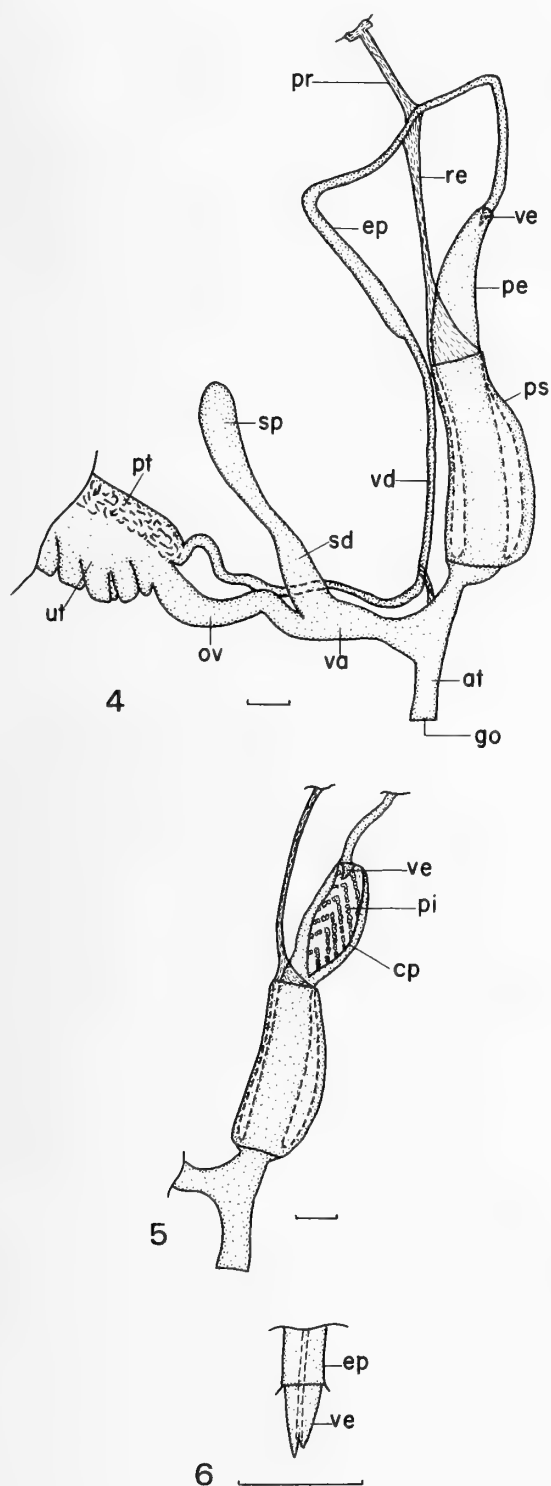
Sheathed part of penis in specimen shown in Figure 4 about 5.0 mm in length, protruding part about 3.5 mm. In other specimens from same locality, sheathed part varying from 4.0 to 5.4 mm (mean 4.5 mm); protruding part varying from 3.4 to 4.6 mm (mean 3.9 mm). Mean ratio of protruding length to sheathed length about 0.87.

Apex of penis containing short, conical, pointed verge 0.5 mm long and 0.3 mm wide at base. Seminal duct opening into penial chamber at tip of verge; tip of verge split into two opposing lips about 0.1 mm long (Figure 6).

Spermathecal duct relatively small and narrow, tightly appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 2.5 mm long, about 1.0 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca.

Spermatheca elongate-ovate, rather slender in fully mature specimens, narrowly cylindrical in less mature individuals, about 3.5 mm long, with rounded tip.

Type material: Holotype: ANSP 11142a (BAKER, 1962). Paratype: UCM 16202 (WU & BRANDAUER, 1982).



Explanation of Figures 4 to 6

Figures 4–6. *Vespericola pilosus* (Henderson). Drawings made from projections of stained whole mounts. Figure 4. Anterior portion of reproductive system, SBMNH 36089, CALIFORNIA: San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon, W. B. Miller coll., 24 August 1991. Figure 5. Penis with protruding portion opened to show verge and pa-

Distribution: CALIFORNIA: San Francisco City and County (ANSP, SBMNH, UCM): Presidio (CAS); Lobos Creek (CAS); near Mountain Lake (CAS); Golden Gate Park (CAS); Lake Merced (CAS). San Mateo County: N slope of San Bruno Mountain facing Guadalupe Canyon (BR, SBMNH); Colma (BR, CAS); Half Moon Bay (SBMNH); canyon back of Half Moon Bay (CAS); Pilarcitos Creek (CAS); Purisima Creek Canyon near mouth of Walker Gulch (BR); San Gregorio (CAS).

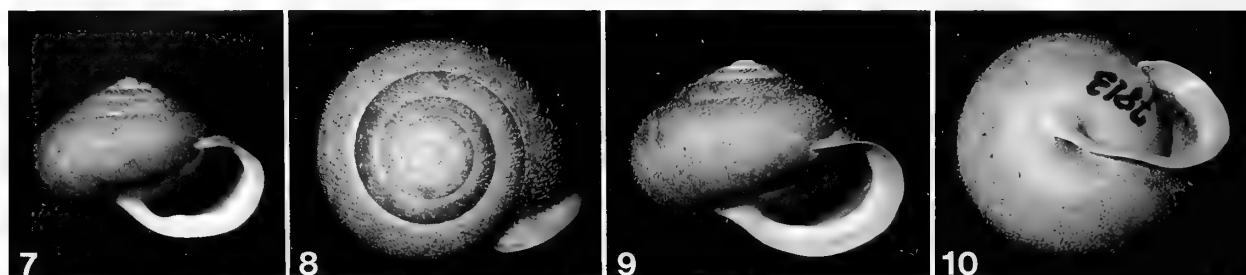
Remarks: The type locality of *Vespericola pilosus* is San Francisco, with no more exact location specified. The species is not known to have been collected within the city limits of San Francisco in recent years; we have searched the San Francisco localities cited above, and others, without finding it. Given the extent of habitat modification in the urban environment, it is unlikely that the type population is still extant. However, the species is moderately common on San Bruno Mountain in northern San Mateo County, just across the county line from San Francisco. The coastal brushfield and chaparral vegetation there was at one time continuous with that of the San Miguel Hills of south-central San Francisco. We have therefore based our shell and anatomical observations on samples from San Bruno Mountain and consider them to represent typical *V. pilosus*.

Previous authors used the name *Vespericola* (or *Polygyra*) *columbiana pilosa* to refer to samples with setose periostracum, whatever their provenance. The name was not applied in the sense of a geographically delimited subspecies. HENDERSON (1928:143) stated, "this race ranges from Alaska to San Francisco Co., Cal." A periostracum with setae occurs in specimens from Alaska to central California and is, in fact, the predominant condition throughout the range of *V. columbianus*. Topotypic and near-topotypic specimens of *V. columbianus* collected by the junior author are setose. We have not yet located any populations characterized by absence of setae, and consider the taxonomic significance of this character to be undemonstrated.

However, specimens from San Francisco and vicinity differ in reproductive system anatomy and details of shell shape from samples from farther north. Populations from the San Francisco peninsula (which include the type population of *Polygyra columbiana pilosa* Henderson) are here assigned to *Vespericola pilosus*, which is separated as a distinct species; populations from Marin County are described as a new species, *V. marinensis*. We provisionally

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pilose pilasters, SBMNH 36090, collection data same as above. Figure 6. Verge and part of epiphallus, showing seminal duct in dashed lines with opening between apical lips, SBMNH 36091, collection data same as above. Abbreviations for anatomical figures: at, atrium; cp, cut edge of penis; ep, epiphallus; go, genital orifice; ov, oviduct; pe, penis; pi, pilaster; pr, penial retractor; ps, penial sheath; pt, prostate; re, retentor; sd, cavity of penial sheath; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens; ve, verge. Scale lines in anatomical figures = 1 mm.



Explanation of Figures 7 to 10

Figures 7–10. *Vespericola columbianus* (Lea). Figure 7. Shell, SBMNH 36092, WASHINGTON: Clark County: Ridgefield Wildlife Refuge, near Vancouver, under log along trail, W. B. Miller coll., 21 July 1989. Diameter 12.1 mm. Figures 8–10. Shell, SBMNH 36093, WASHINGTON: Pacific County: right bank of Columbia River 0.4 km W of highway bridge to Astoria, Oregon, W. B. Miller coll., 12 July 1989. Top, apertural, and basal views. Diameter 14.0 mm.

refer records from northwestern California and the Pacific Northwest to *V. columbianus*, *sensu lato*, pending a more comprehensive study of the anatomy of samples from throughout its range.

An attempt was made to collect topotypes of *Vespericola columbianus* at Vancouver, Washington. Although the area has been extensively urbanized, one specimen was collected at the Ridgefield Wildlife Refuge north of the city (Figure 7). Upon dissection, its anatomy was found to be too immature for comparative measurements. The following anatomical notes are based on mature specimens collected about 130 km downstream along the right (north) bank of the Columbia River just west of the highway bridge to Astoria, Oregon (Figures 8–10).

Color of living animals tan, darker and grayer on body-stalk. Mantle over lung clear buff, about 20% maculated with black.

Atrium (Figure 11) of moderate length for genus. Penis elongate-conical, largely enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of penial chamber bearing papillose pilasters in diverging V-pattern (Figure 12). Broad peduncular section of about 1.0 mm present between base of sheath and junction with atrium.

Sheathed part of penis about 5.0 mm in length; protruding part about 0.2 mm. Apex of the penis containing short, conical, pointed verge 1.0 mm long and 0.5 mm wide at base. Seminal duct opening into penial chamber at tip of verge through minute slit (Figure 13).

Spermathecal duct short and massive, appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 2.0 mm long, about 1.5 mm in diameter at junction with oviduct, tapering sharply to 0.5 mm constriction at base of spermatheca.

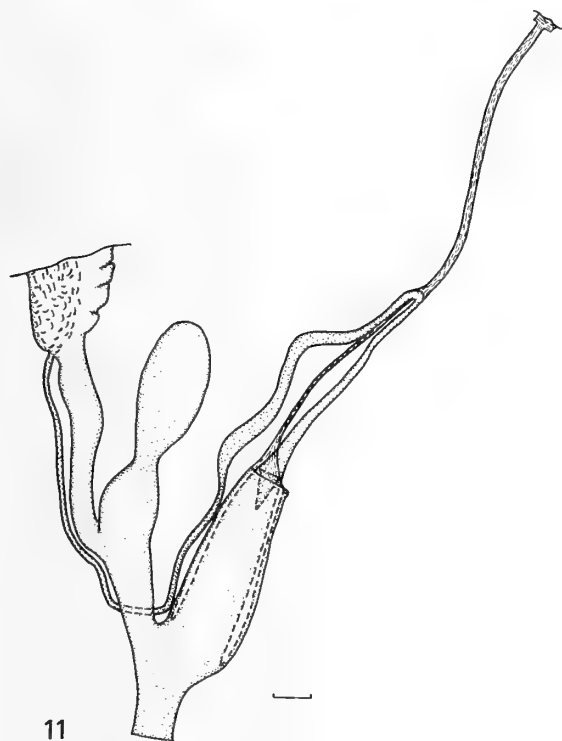
Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 4.0 mm long, with rounded tip.

Numerous additional specimens of *Vespericola columbianus* were examined, ranging from Prince Rupert and the Queen Charlotte Islands, British Columbia, to the valley of the Columbia River, Washington-Oregon. A consideration of the variation within the species over its range is beyond the scope of this paper. However, a summary of characters based on 69 dissected specimens is as follows: mantle over the lung 10–90% maculated with black; sheathed part of penis 3.6–8.5 mm long (mean 5.7 mm); protruding part of penis 0–1.4 mm long (mean 0.6 mm). (In seven specimens from three localities in British Columbia [Bridal Veil Falls, Hope District; Port Hardy, Vancouver Island; and Graham Island, Queen Charlotte Islands], penial sheath extending 0.5–4.2 mm above summit of penis.) Verge 0.8–2.0 mm long; spermathecal duct 1.5–3.0 mm long.

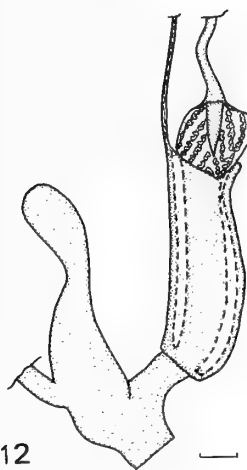
The main anatomical characters that distinguish *Vespericola columbianus* are its stout penial complex, with the sheath completely or almost completely enveloping the penis in mature specimens, and the moderately long, conical, pointed verge at the apex of the penial chamber. The spermathecal duct is short and thick at its junction with the oviduct.

Vespericola pilosus differs anatomically from *V. columbianus* by the long protruding portion of its penis, its much shorter verge, and its narrower, more slender spermathecal duct and spermatheca. It is distinguished from *V. marinensis*, next described, by having the sheathed length of the penis equal to or greater than the protruding length, a verge half or less the length of the verge of *V. marinensis*, and a more slender spermathecal duct. Table 1 summarizes the major differences among these taxa.

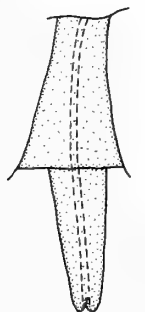
The periphery of the shell of *Vespericola pilosus* is broadly rounded; that of *V. columbianus* is usually weakly subangulate to at least the last 0.5 whorl. The periostracal setae of *V. pilosus* tend to be denser (19–30/mm²) than those of *V. columbianus* (7–19/mm² in the specimens examined) and much denser than in *V. marinensis* (7–10/mm²). PILSBRY (1940) considered the typical form of *V. columbianus* generally to lack setae, but all specimens we have



11



12



13

seen have (or originally had) setae, although they have been rubbed off some museum specimens.

The habitat of *Vespericola pilosus* includes moist spots in coastal brushfield and chaparral vegetation; under leaves of cow-parsnip (*Heracleum lanatum*); around spring seeps; in leafmold along streams; and in alder woods.

The earlier citation of the taxon as "*Vespericola pilosa*" by BAKER (1962) was not a taxonomic revision but merely a convention of that publication, a list of type material in the ANSP.

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name "brushfield hesperian."

Vespericola marinensis Roth & Miller, sp. nov.

(Figures 14–19)

Vespericola columbiana pilosa (Henderson): PILSBRY, 1940: 896–898 (in part; records from Marin County, California, only); INGRAM, 1946:92 (in part); INGRAM & LOTZ, 1950:25–26 (in part). *Non Vespericola pilosus* (Henderson, 1928).

Diagnosis: A small to medium-sized *Vespericola* with depressed-helicoid to broadly conical, narrowly umbilicate shell, 5.4–5.9 whorls, 7–10 periostracal setae/mm², and no parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.6; verge 0.7–1.8 mm long, conical, ending in 0.1 mm opposing lips.

Description of shell: Shell small to medium-sized for the genus (diameter 10.5–15.0 mm) depressed-helicoid to broadly conical, narrowly umbilicate, with 5.4–5.9 whorls. Spire straight-sided or very weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5–1.8, with prominent, sharp to rounded, radial wrinkles surmounted by smooth, hemispheric to radially elongate papillae. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae and close-set, regular granulation with collabral trend. Periostracum bearing slender setae in diagonal, often steeply descending, rows; setae 7–10/mm², approximately 0.3–0.35 mm long

Explanation of Figures 11 to 13

Figures 11–13. *Vespericola columbianus* (Lea). Drawings made from projections of stained whole mounts. Figure 11. Anterior portion of reproductive system, SBMNH 36094, WASHINGTON: Pacific County: right bank of Columbia River just W of highway bridge to Astoria, Oregon, W. B. Miller coll., 12 July 1989. Figure 12. Penis with protruding portion opened to show verge and papillose pilasters, SBMNH 36095, BRITISH COLUMBIA: Naikoon Provincial Park, Graham Island, Queen Charlotte Islands, W. B. Miller and E. S. Miller coll., 22–24 June 1991. Specimen slightly immature as indicated by small spermatheca and penial sheath not enveloping entire penis. Figure 13. Verge and part of epiphallus, showing seminal duct in dashed lines with opening in apical slit, SBMNH 36096, collection data same as for preceding specimen.



Explanation of Figures 14 to 16

Figures 14–16. *Vespericola marinensis* Roth & Miller, sp. nov. Shell, holotype, SBMNH 36080, CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990. Top, apertural, and basal views. Diameter 12.2 mm.

on spire and shoulder of body whorl, erect or curving away from direction of coiling, sometimes with recurved tip, moderately broadened at base. Surface between setae densely, smoothly granulose on spire and body whorl and collabrally wrinkled. Periphery simply rounded, not subangulate. Base tumid, densely papillose; with setae extending into umbilicus. Umbilicus contained about 13–16 times in diameter. Body whorl deflected downward except immediately behind aperture, sharply constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of 25° to 45° to shell axis. Lip turned outward and expanded, somewhat reflected at base; basal and outer lips sometimes thickened submarginally. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering $\frac{1}{5}$ to $\frac{1}{3}$ of umbilicus. Periostracum warm brown; lip pale tan to white.

Dimensions of holotype: Diameter (exclusive of expanded lip) 12.2 mm, height 8.7 mm, whorls 5.6.

Description of soft anatomy: The holotype and 66 additional specimens were dissected.

Color of living animals tan to brown on foot, darker and grayer on body-stalk. Mantle over lung 15–30% maculated with black.

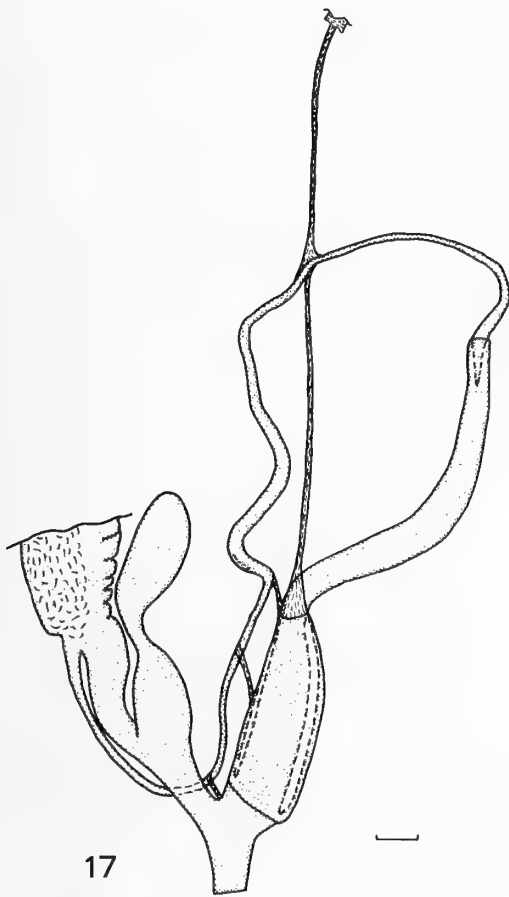
Atrium (Figure 17) of moderate length for genus. Penis elongate-conical, anterior, basal portion enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Interior of the penial chamber bearing papillose pilasters in diverging V-pattern (Figure 18). Short, broad peduncular section of about 0.8 mm present between base of sheath and junction with atrium.

Sheathed part of penis in specimen shown in Figure 17 about 4.8 mm in length, protruding part about 8.8 mm. In remaining specimens, sheathed part varying from 3.4

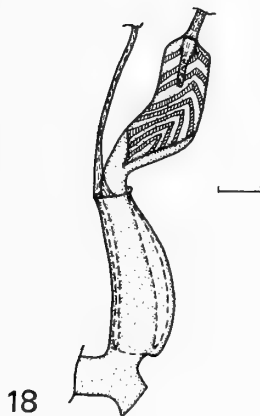
Table 1

Summary of dimensions (in mm), ratios, and selected characters in *Vespericola columbianus*, *V. pilosus*, *V. marinensis*, and *V. orius*. Statistics are range with mean in parentheses. Only adult specimens included.

Character	<i>V. columbianus</i>	<i>V. pilosus</i>	<i>V. marinensis</i>	<i>V. orius</i>
Mantle over lung, coverage by dark maculation	10–90%	10–50%	15–30%	30–40%
Sheathed part of penis	3.6–8.5 (5.7)	4.0–5.4 (4.5)	3.4–6.0 (4.4)	2.5–3.0 (2.7)
Protruding part of penis	0.0–1.4 (0.6)	3.4–4.6 (3.9)	4.8–10.8 (7.0)	—
Ratio of protruding part to sheathed part	mean \approx 0.11	mean \approx 0.87	mean \approx 1.6	—
Verge, length	0.8–2.0 (1.2)	0.5–0.6 (0.5)	0.7–1.8 (1.1)	0.15–0.20 (0.18)
Verge, end	minute slit	apical slit forming 0.1 mm lips	apical slit forming 0.1 mm lips	conical
Spermathecal duct	1.5–3.0 (2.6), massive	2.5, slender	\approx 3.0, massive	\approx 2.0, slender
Spermatheca, length	4.0	3.5	3.2	\approx 2.7
Peduncular section of penis	1.0	2.0	0.8	1.0
Periphery	weakly subangulate	broadly rounded	broadly rounded	usually weakly subangulate
Periostracal setae/mm ²	7–19	19–30	7–10	11–17



17



18



19

to 6.0 mm (mean 4.4 mm); protruding part varying from 4.8 to 10.8 mm (mean 7.0 mm). Mean ratio of protruding length to sheathed length about 1.6.

Apex of penis containing short, conical, pointed verge varying from 0.7 to 1.8 mm long, 0.3 mm wide at base. Seminal duct opening into penial chamber at tip of verge through apical slit which forms two opposing lips about 0.1 mm long (Figure 19).

Spermathecal duct massive, tightly appressed to free oviduct (which is smaller in diameter and branches from it), cylindrical-conic, about 3.0 mm long, about 1.3 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 3.2 mm long, with rounded tip.

Type material: Holotype: SBMNH 36080 (shell and dissected anatomy), CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990.

Paratypes: SBMNH 36081 (4 shells and stained whole mount of reproductive system), from same locality as holotype. Additional paratypes (all, CALIFORNIA: Marin County:), SBMNH 36082 (4), along Bear Valley Trail ca. 2.0 km inland from Arch Rock, under logs and bark, W. B. Miller coll., 1 January 1989. SBMNH 36083 (1), along Bear Valley Trail, ca. 0.8 km from Arch Rock, W. B. Miller coll., 25 July 1989. SBMNH 36084 (1), along Bear Valley Trail, ca. 0.8 km from Arch Rock, under log, W. B. Miller coll., 20 September 1990. SBMNH 36085 (2), Bear Valley Trail, W. B. Miller and E. S. Miller coll., 24–29 April 1988. SBMNH 36086 (7), Bear Valley Trail, between Wilderness boundary and Arch Rock, under logs along trail, W. B. Miller coll., 13 November 1989. Paratypes also deposited in ANSP, CAS, LACM, and USNM.

Referred material: CALIFORNIA: Marin County: Dillon Beach (CAS); Tomales Point (CAS); head of first large east-draining draw N of Whites Gulch (BR, SBMNH), McClures Beach parking area (BR), side canyon of Home Ranch Creek Canyon (BR), Muddy Hollow Trail (SBMNH); Kehoe Beach (BR, SBMNH) (all, Point Reyes Peninsula); Inverness (BR, SBMNH); Point Reyes Station (CAS); Olema Creek (BR); 1.6 km SW of California Hwy. 1 bridge over Walker Creek, E side of Tomales Bay

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Explanation of Figures 17 to 19

Figures 17–19. *Vespericola marinensis* Roth & Miller, sp. nov. Drawings made from projections of stained whole mounts. Figure 17. Anterior portion of reproductive system of holotype, SBMNH 36080, CALIFORNIA: Marin County: Bear Valley Trail, Point Reyes, W. B. Miller coll., 23 April 1990. Figure 18. Penis with protruding portion opened to show verge and papillose pilasters, SBMNH 36087, CALIFORNIA: Marin County: Muddy Hollow Trail, Point Reyes, W. B. Miller coll., 20 April 1990. Figure 19. Verge, SBMNH 36088, CALIFORNIA: Marin County, Alpine Dam, W. B. Miller and B. Roth coll., 16 January 1991.



Explanation of Figures 20 to 22

Figures 20–22. *Vespericola orius* (Berry). Shell, BR 330, CALIFORNIA: El Dorado County: Eagle King Mine, Grizzly Flats, E. P. Chace and E. M. Chace coll., autumn 1938. Top, apertural, and basal views. Diameter 13.0 mm.

(BR); Walker Creek, 0.4 km above mouth of Chileno Creek (BR); Taylorville (SBMNH); San Geronimo Creek near Forest Knolls (BR); Mesa Road, ca. 3 km NW of Bolinas (BR, SBMNH); debris above high tide line, N end of Bolinas Lagoon (BR) Lagunitas Creek, 0.3 km below Alpine Dam (BR, SBMNH); Alpine Dam (SBMNH); near Stinson Beach (CAS); near Fairfax (CAS); Ross (SBMNH); San Rafael (CAS); Muir Woods (CAS); Sausalito (SBMNH); Point Bonita (CAS).

Remarks: In the type material, adult shell diameter ranges from 11.6 to 14.0 mm (mean of 24 specimens including holotype, 12.57 mm); height, 8.0 to 9.5 mm (\bar{x} = 8.65 mm); height-diameter ratio, 0.63 to 0.73 (\bar{x} = 0.689); number of whorls, 5.4 to 5.9 (\bar{x} = 5.68). The largest shells examined are from Walker Creek, 0.4 km above mouth of Chileno Creek, reaching 15.0 mm in diameter and 9.6 mm in height. Small shells, adult at 10.5 mm diameter, occur on the northern part of the Point Reyes Peninsula, as at Tomales Point and near Whites Gulch.

The shell of *Vespericola marinensis* differs from that of *V. pilosus* and *V. orius* in having fewer setae per millimeter and in having the surface between the setae densely covered by smooth, round to radially elongated granules. In *V. pilosus* the granulation is sharper on the spire, usually becoming weak or obsolete on the body whorl. In *V. orius* granulation is weak throughout.

Vespericola marinensis is distinguished anatomically from other species by its moderately long, pointed verge, with apical slit forming two opposing lips, in a narrowly elongated penis protruding for more than half of its length from the basal penial sheath. It differs from *V. pilosus* by its longer verge (more than twice the length of the *V. pilosus* verge) and by its longer protruding part of the penis. It differs from *V. columbianus* by the much longer protruding part of the penis, which is never completely enclosed by the penial sheath.

The habitat includes moist spots in coastal brushfield and chaparral vegetation; under leaves of cow-parsnip (*Heracleum lanatum*); around spring seeps; in leafmold along streams; in alder woods; and in mixed evergreen forest.

INGRAM & LOTZ (1950) reported *Vespericola columbiana pilosa* from Hacienda, Sonoma County. PILSBRY (1928) reported it (as *Polygyra*) from Russian River, presumably in Sonoma, rather than Mendocino, County. We have not examined specimens from these localities, and do not know whether they represent northern records of *V. marinensis*. The occurrences are within the range of *Vespericola megasoma* (Pilsbry, 1928).

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name “*Marin hesperian*.”

Etymology: The species is named for Marin County.

Vespericola orius (Berry, 1933)

(Figures 20–24)

Polygyra columbiana oria BERRY, 1933:15, pl. 2, figs. 11, 11a.
Vespericola columbiana oria (Berry): PILSBRY, 1940:900–901, fig. 516; INGRAM, 1946:92.

Diagnosis: A medium-sized *Vespericola* with depressed-helicoid to broadly conical, umbilicate shell, 5.2–6.25 whorls, 11–17 periostracal setae/mm², and no parietal lamella. Penis short, stout, completely enclosed in sheath, apical portion slender and tubular, containing 0.15–0.20 mm long, conical verge.

Description of shell: Shell thin, medium-sized for the genus (diameter 11.6–16.4 mm) depressed-helicoid to broadly conical, umbilicate, with 5.2–6.25 whorls. Spire straight-sided or very weakly convex; whorls rounded, suture moderately impressed. Embryonic whorls 1.5–1.8, most often with prominent, sharp, radial wrinkles surmounted by smooth, round to radially elongate papillae, but wrinkles sometimes faint and surface between papillae smooth. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae, very slightly granular. Periostracum bearing slender setae in gently descending rows; setae 11–17/mm², approximately 0.3 mm long on spire and shoulder of body whorl, erect or curving away

from direction of coiling, not greatly broadened at base but sometimes with triangular basal lamina abaperturally. Surface between setae finely radially wrinkled, locally with patches of minute granulation. Periphery usually with a trace of angulation, at least before last 0.5 whorl; sometimes simply rounded. Base tumid, with setae shorter than on spire, extending into umbilicus. Umbilicus contained 11–14 times in diameter. Body whorl weakly to moderately deflected downward, constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile, at angle of about 35° to shell axis. Lip turned outward and reflected, especially at base; not conspicuously thickened. Parietal lamella absent. Inner part of basal lip curved or angled forward, moderately dilated, covering $\frac{1}{5}$ to $\frac{1}{2}$ (usually $\frac{1}{3}$ or less) of umbilicus. Periostracum warm brown; lip pinkish buff.

Description of soft anatomy: Twelve specimens were dissected.

Color of living animals tan, darker and grayer on body-stalk. Mantle over lung clear buff, 30–40% maculated with black.

Atrium (Figure 23) of moderate length for genus. Penis short and stout, completely enclosed in thin sheath adnate to base. Apical part of penis slender and tubular, of same diameter as epiphallus, containing minuscule verge. Sheath extending above summit of penis, enclosing portion of epiphallus. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Short peduncular section of about 1.0 mm present between base of sheath and junction with atrium.

Length of penis, from base to verge, in figured specimen about 2.5 mm; sheathed part of epiphallus about 1.3 mm; total sheath length 3.8 mm. In other specimens, length of penis varying from 2.5 to 3.0 mm (mean 2.7 mm; total length of the sheath varying from 3.4 to 4.2 mm (mean 3.9 mm).

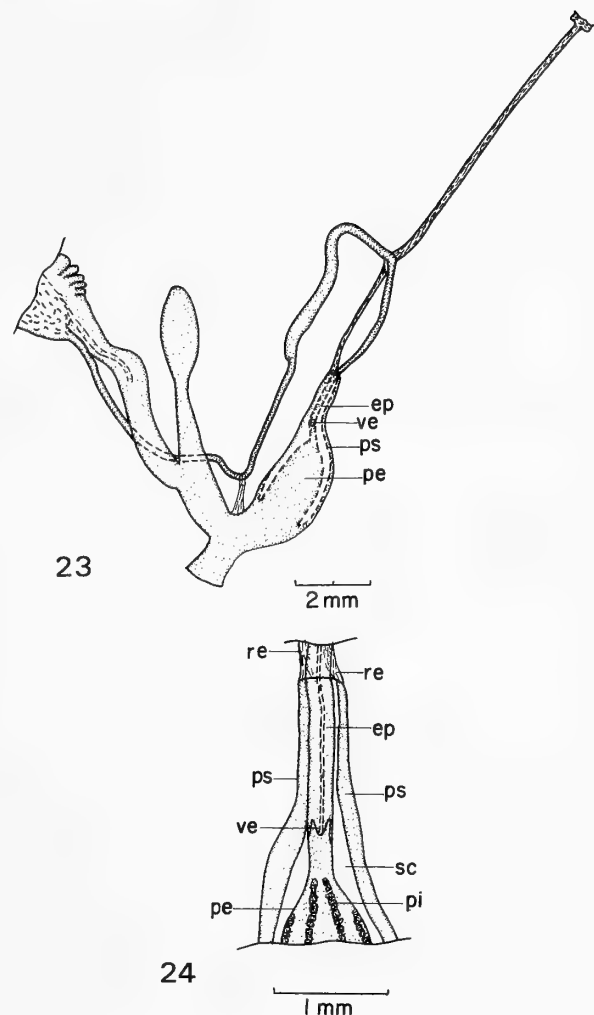
Verge within narrow, tubular, apical portion of the penis, about 0.15 to 0.20 mm long, 0.20 mm wide at base (Figure 24). Seminal duct opening into penis through tip of verge.

Spermathecal duct small and narrow, tightly appressed to free oviduct, which is of equal diameter and branches from it, cylindrical-conic, about 2.0 mm long, about 0.7 mm in diameter at junction with oviduct, tapering gradually to 0.3 mm constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 2.7 mm long, with rounded tip.

Type material: Holotype: SBMNH 34203, CALIFORNIA: El Dorado County: canyon of South Fork of American River near Riverton.

Paratypes: CAS 064120, CAS 066614, SBMNH 34204, from same locality as holotype.



Explanation of Figures 23 and 24

Figures 23, 24. *Vespericola orius* (Berry). Drawings made from projections of stained whole mounts. Figure 23. Anterior portion of reproductive system, SBMNH 36097, CALIFORNIA: El Dorado County: along left bank of North Fork of Cosumnes River at crossing of Cosumnes Mine Road, W. B. Miller coll., 21 January 1991. Figure 24. Enlarged section of epiphallus and apical portion of penis to show location of verge, SBMNH 36098, collection data same as above.

Distribution: CALIFORNIA: El Dorado County: Placerville (CAS); near Camp Creek, 4.8 km E of Pleasant Valley (CAS); along left bank of North Fork of Cosumnes River at crossing of Cosumnes Mine Road, W. B. Miller coll., 21 January 1991 (SBMNH); Eagle King Mine, near Grizzly Flat (CAS, BR); South Fork of American River near Riverton (CAS).

Remarks: The epiphallus and the apical part of the penis form a continuous tube of constant diameter, with no external differentiation. There is no bulge or swelling at the level of the verge. Only at about 0.5 mm below the verge does the penis enlarge abruptly into a capacious cavity.

This gives the appearance that the verge is located well up in the epiphallus; but, by convention, the portion of the male sperm-delivering duct below the base of the verge and above the atrium, everted in copulation, is defined as the penis. It seems probable to us that the slender part of the duct below the base of the verge is homologous with the summit of the penial sac in other species of *Vespericola*.

Vespericola orius is distinguished anatomically from other species by its minuscule verge located in a narrow, tubular, prolongation of the apex of the penial chamber; by its short, stout penis in a penial sheath overlapping a sizeable part of the epiphallus; and by its small, narrow spermathecal duct.

The inner end of the basal lip of the aperture is more distinctly angled forward than in *Vespericola pilosus* and covers, on the average, less of the umbilicus. The surface between the periostracal setae is less granulose than in *V. pilosus*, especially on the spire.

For purposes of the American Fisheries Society list of the common names of mollusks (TURGEON *et al.*, 1988) and other administrative uses, we propose the name "El Dorado hesperian."

OTHER RECORDS OF *Vespericola columbianus* IN CALIFORNIA

In museum collections, shells in which the inner lip is not markedly dilated over the umbilicus are often identified as *Vespericola columbianus*. On the basis of our previous findings, we believe such identifications require confirmation by dissection.

PILSBRY (1940) reported *Vespericola columbianus pilosus* from Crescent City, Del Norte County, and San Pablo, Contra Costa County, California. Our collecting along the coast of Del Norte County has not turned up any *V. columbianus*, but rather *Vespericola megasoma*, *Vespericola euthales* (Berry, 1939), and two new species, outwardly similar to *V. megasoma*, that will be described and discussed in a future paper.

Museum collections contain samples resembling *Vespericola pilosus* from several localities in Contra Costa and Alameda counties. The shells are, in general, more depressed and more widely umbilicate than those of *V. pilosus* from the San Francisco Peninsula, with the inner part of the basal lip angled rather sharply forward. A parietal lamella is absent. We are in the process of trying to locate living populations for anatomical data.

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Slugs of Portugal. III. Revision of the Genus *Geomalacus* Allman, 1843 (Gastropoda: Pulmonata: Arionidae)

by

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Abstract. This study revises the genus *Geomalacus* in Portugal and compares specimens found there with those found in Ireland, where it is represented by *Geomalacus maculosus*, and specimens encountered in Spain. The anatomy of the specimens is also described with the belief that they all belong to three species: *Geomalacus maculosus*, *G. oliveirae*, and *G. anguiformis*.

INTRODUCTION

The genus *Geomalacus* (type species *G. maculosus*) was created by ALLMAN in 1843 to include certain long-bodied slugs with large palish marks, pneumostome on the lower third of the shield, genital orifice between the shield and the lower right tentacle, very small caudal mucus pore, and quite solid, flat limacella (GERMAIN, 1930). The seminal receptacle of species in this genus does not open directly into the atrium; rather it does so in a large (in most cases) vaginal diverticulum.

POLLONERA (1890) considered the subgenus *Geomalacus* as typical of pale-spotted slugs, with the sexual organs arranged differently from striped species. He formed the subgenus *Arrudia* for species of *Geomalacus* that have dark lateral bands instead of spots on the back, and whose genital apparatus resembles that of *Arion*. *Arrudia* is distinguished from *Ariunculus* by its smaller caudal gland, its reproductive apparatus, and by the presence of limacellae. Pollonera included *Geomalacus anguiformis* Morelet, 1845, *Geomalacus squammantinus* Morelet, 1845, and *Geomalacus oliveirae* Simroth, 1891, in the subgenus *Arrudia*, and *G. maculosus* in the subgenus *Geomalacus*.

Four species of *Geomalacus* have been reported or described in Portugal: *G. (Geomalacus) maculosus* Allman, 1843, *G. (Arrudia) anguiformis* (Morelet, 1845), *G. (Arrudia) oliveirae* Simroth, 1891, *G. (Geomalacus) grandis* Simroth, 1893.

PREVIOUS WORK IN THE IBERIAN PENINSULA

Geomalacus maculosus Allman, 1843

Geomalacus maculosus was described by ALLMAN in 1843 from specimens collected at Carogh Lake in County Kerry, Ireland.

Dr. Paul Fischer reported the abundance of this species in Asturias (NW Spain) and in 1868 Lucas von Heyden found a single specimen in Santa Albas (Asturias) (in TAYLOR [1907]). SILVA & CASTRO (1873) had found an individual adult in the Monte de Sao Silvestre, near Viana do Castelo, which they described as *Letourneuxia lusitana*, later to be synonymized as *Limax lusitanus* by MORELET (1877). SIMROTH (1891) made observations of 40 juveniles collected in the Serra de Gerês in north Portugal. He admitted that this was not the first report of the species in Portugal.

TAYLOR (1907) and HIDALGO (1916) recompiled the previous reports of this species in Portugal and Spain. QUICK (1960) said this species was found in Portugal, Spain, Vannes (Brittany, France) and southeastern Ireland. NOBRE (1941) found a single specimen close to Porto, and SEIXAS (1976) found several in the far north of Portugal, near the border with Galicia.

Geomalacus grandis Simroth, 1893

SIMROTH (1893) described a new species of the genus *Geomalacus* under the name *G. grandis* for specimens recovered in the Serra da Estrela. NOBRE (1941) indicated the places where it had been found, but he did not find any specimens of this species. CASTILLEJO (1981b) redescribed *G. grandis* using material from different parts of Galicia (NW Spain), and CASTILLEJO & MANGA (1986) provided a list of the locations in Galicia and Portugal

where this species appears. OUTEIRO (1988) found it at O Courel, Lugo (Spain).

PLATTS & SPEIGHT (1988) thought it highly likely that the Portuguese material of *Geomalacus grandis* belonged to *G. maculosus*, as did the Spanish specimens they studied. Both authors went to the Serra da Estrela (Portugal) in October 1987 to collect material, but failed to find specimens of *Geomalacus*; they deduced that both species were possible synonyms. On the same field trip they found specimens of *G. grandis* at Padrón (La Coruña, Spain), and after comparing them with their specimens of *G. maculosus*, they considered that the Galician *G. grandis* was the same as the *G. maculosus* of Ireland.

Geomalacus anguiformis (Morelet, 1845),
Limax squammantinus (Morelet, 1845), and
Limax viridis (Morelet, 1845)

MORELET (1845) described *Limax anguiformis* based on material collected in the Serra de Monchique (Portugal) and *L. squammantinus* and *L. viridis* from specimens collected in the Serra do Caldeirao (Portugal). POLLONERA (1890) described the internal anatomy of *Geomalacus anguiformis* and *G. squammantinus* and considered *G. squammantinus* as a juvenile form of *G. anguiformis*. SIMROTH (1891) indicated that the form of its wrinkles on the back, its inability to contract greatly, the slowness of movement, and the fact that the head is visible only with the tentacles extended, put it in the genus *Geomalacus*. For Simroth *L. squammantinus* and *L. viridis* were juvenile forms of *G. anguiformis*.

SIMROTH (1893) thought that *Geomalacus viridis* (Morelet, 1845) was a doubtful species; he interpreted it as a juvenile of *G. anguiformis* on the basis of its appearance. He added that *G. viridis* should be rejected since its anatomy was then totally unknown, making any logical assignment to a species impossible. SIMROTH's (1893) report was the last mention of *G. anguiformis* until it was collected by WIKTOR & PAREJO (1989) in Robledo del Mazo (Tolledo, Spain), the first report of this species in Spain.

Geomalacus oliveirae Simroth, 1891

SIMROTH (1891), referring to two specimens of Arionidae from Guarda (Portugal) sent by Mr. Paulino d'Oliveira, thought that externally they were very similar to *Geomalacus anguiformis*, and that they were probably an intermediate form between it and *G. maculosus*. He described this species in detail, naming it *Geomalacus oliveirae* and comparing it to anatomically close species. Two years later SIMROTH (1893) commented that the description of this species showed that the Portuguese fauna, in relation to this new genus, had still not been fully researched. There are no more references to *G. oliveirae* until NOBRE (1941) stated that he knew no diagnosis for it. It is absent from SEIXAS' (1976) account of the Portuguese fauna.

In SIMROTH's (1891, 1893) view the species of the genus *Geomalacus* are distributed along the mountain chains that

go from east to west across the Iberian Peninsula, and he stated that it was strange to find at least one of them, *G. maculosus*, along the southern rim of Ireland. According to Simroth, in Spain the northern species, *G. maculosus*, should appear in the Cantabrian cordillera, *G. oliveirae* should appear in the Castilian mountains, and *G. anguiformis* in the Betic system. In 1893 SIMROTH urged a study of the genus *Geomalacus* in order to make its taxonomic position clear and to demonstrate or disprove that it was separated by mountain chains. NOBRE (1941) did just that and attempted to study the species reported in Portugal; he merely stated that they were introduced species, since he could only find one specimen of *G. maculosus*.

MATERIALS AND METHODS

Specimens were gathered by day and night. During the day hiding places occupied by *Geomalacus* were sought, so that at night the slugs could be captured when they emerged or fed. Transport, fixing, conservation, and dissection were performed according to the methodology used by ADAM (1960) and CASTILLEJO (1981a).

Scale drawings were made with the aid of a tracing screen attached to a binocular viewer. The scales in each drawing were calculated using a piece of paper with millimeter squares placed on the sample.

RESULTS

Specimens of the genus *Geomalacus* were collected at several sites in mainland Portugal, including the type localities of the species described in Portugal. It was also possible to study a specimen of *G. maculosus* found at Carugh Lake, in Ireland, and deposited in the British Museum (No. 70.12.23.45).

Drawing on the bibliographic data available to us concerning *Geomalacus*, not only for the Iberian Peninsula but also for the rest of Europe (no reference has ever been made to this species outside Europe), we consider that the differences, which Simroth used for separating *G. maculosus* and *G. grandis*, are not significant differences and that *G. maculosus* and *G. grandis* are the same species, with the name *G. maculosus* having priority and *G. grandis* being a junior synonym. As regards *G. anguiformis* and *G. oliveirae*, we believe that both are good species.

From the study of all the specimens collected in Portugal we have reached the same conclusion that we reached from studying the literature; namely that, these specimens can be assigned to three species: *Geomalacus maculosus*, *G. anguiformis*, and *G. oliveirae*.

Geomalacus maculosus Allman, 1843

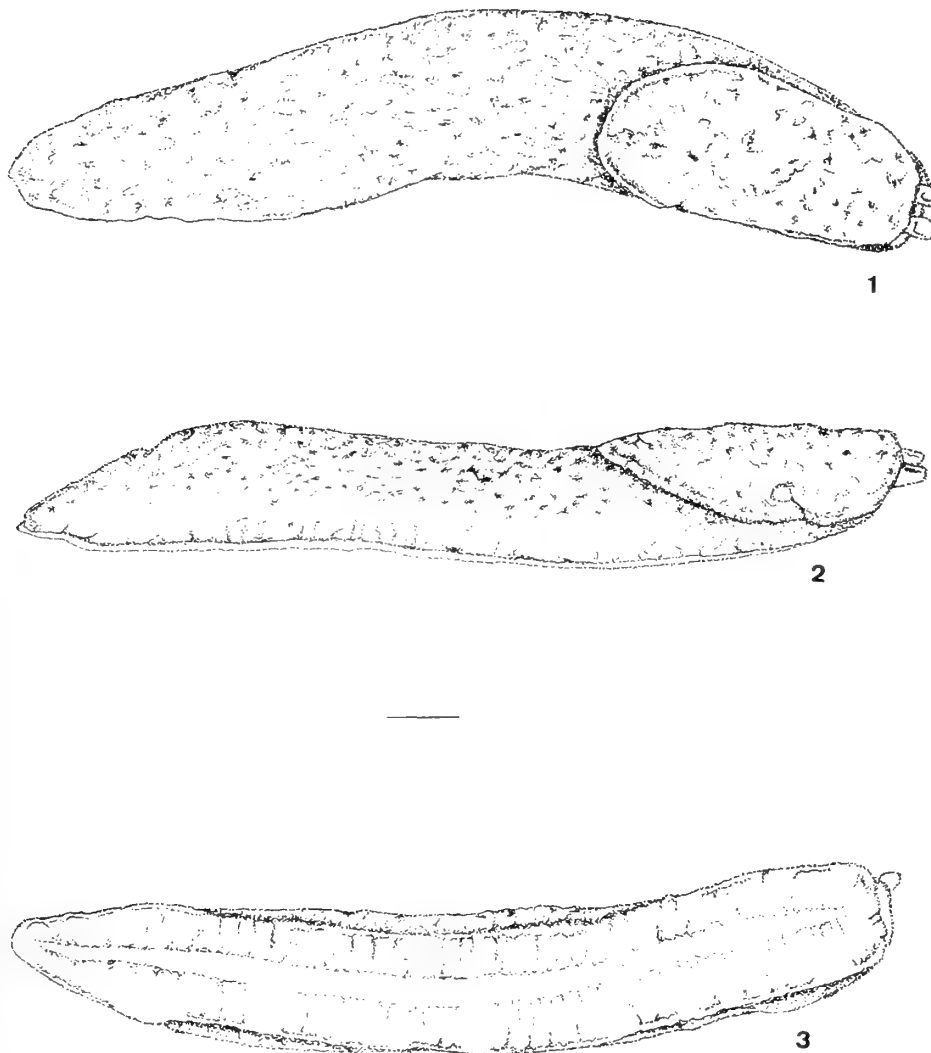
(Figures 1–13)

Letourneuxia lusitana Silva & Castro, 1873

Limax lusitanus Morelet, 1877

Geomalacus lusitanus Pollonera, 1890

Geomalacus grandis Simroth, 1893



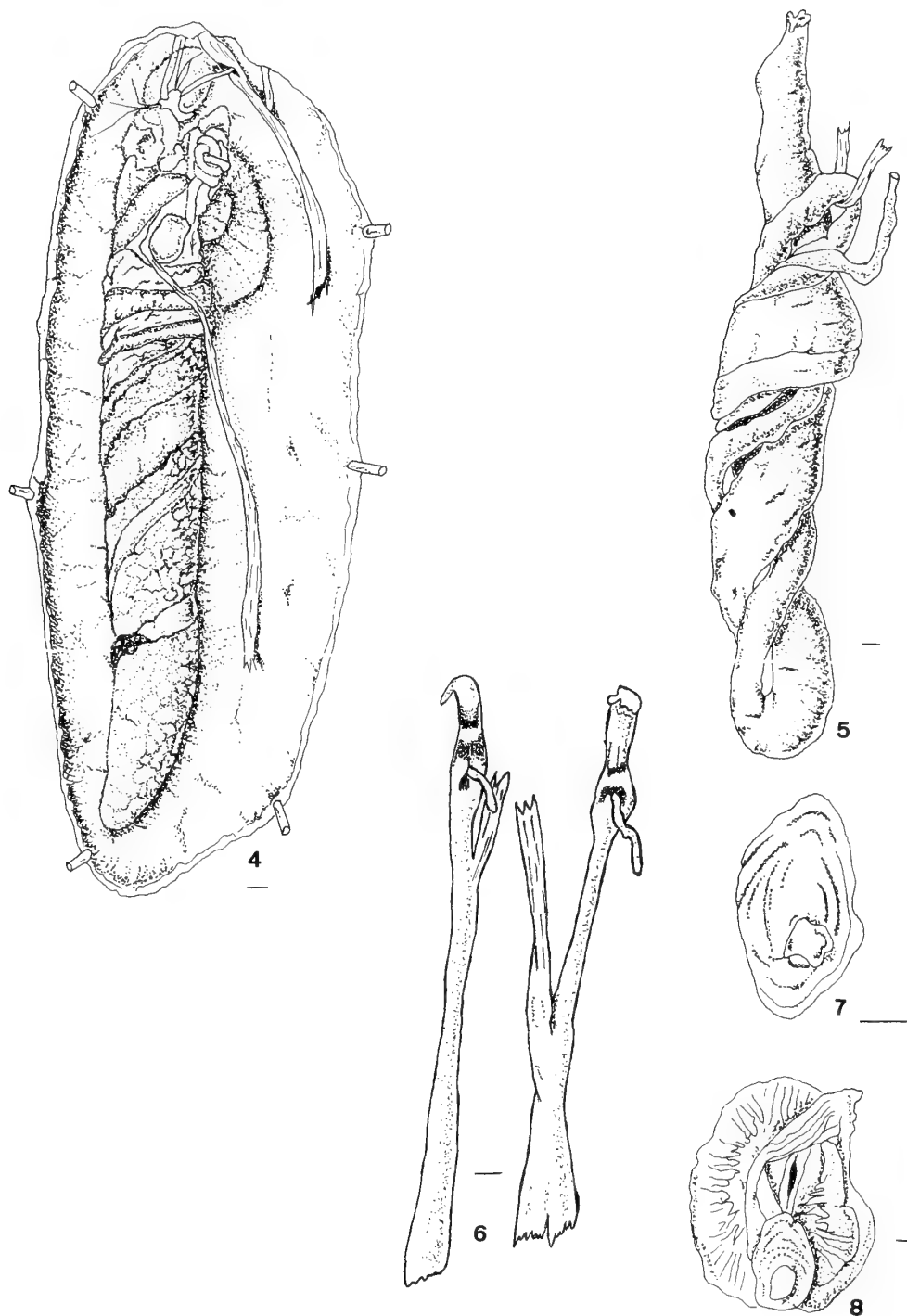
Explanation of Figures 1 to 3

Figures 1–3. *Geomalacus maculosus*. Dorsal, lateral, and ventral views of a specimen from the Serra da Estrela (type locality of *Geomalacus grandis*). Scale 5 mm.

Description and iconography: *Geomalacus grandis* SIMROTH, 1893:291; pl. 1, fig. 1; pl. 2, figs. 1–3; NOBRE, 1930: 65; pl. 1, fig. 4; NOBRE, 1941:74; pl. 2, fig. 4; CASTILLEJO, 1981:105; pl. 15, 16; pl. 125, figs. 1–4, 6. *Geomalacus maculosus* Allman, 1843: ALLMAN *et al.*, 1846:297, pl. IX; PLATTS & SPEIGHT, 1988:417, figs. 1–7.

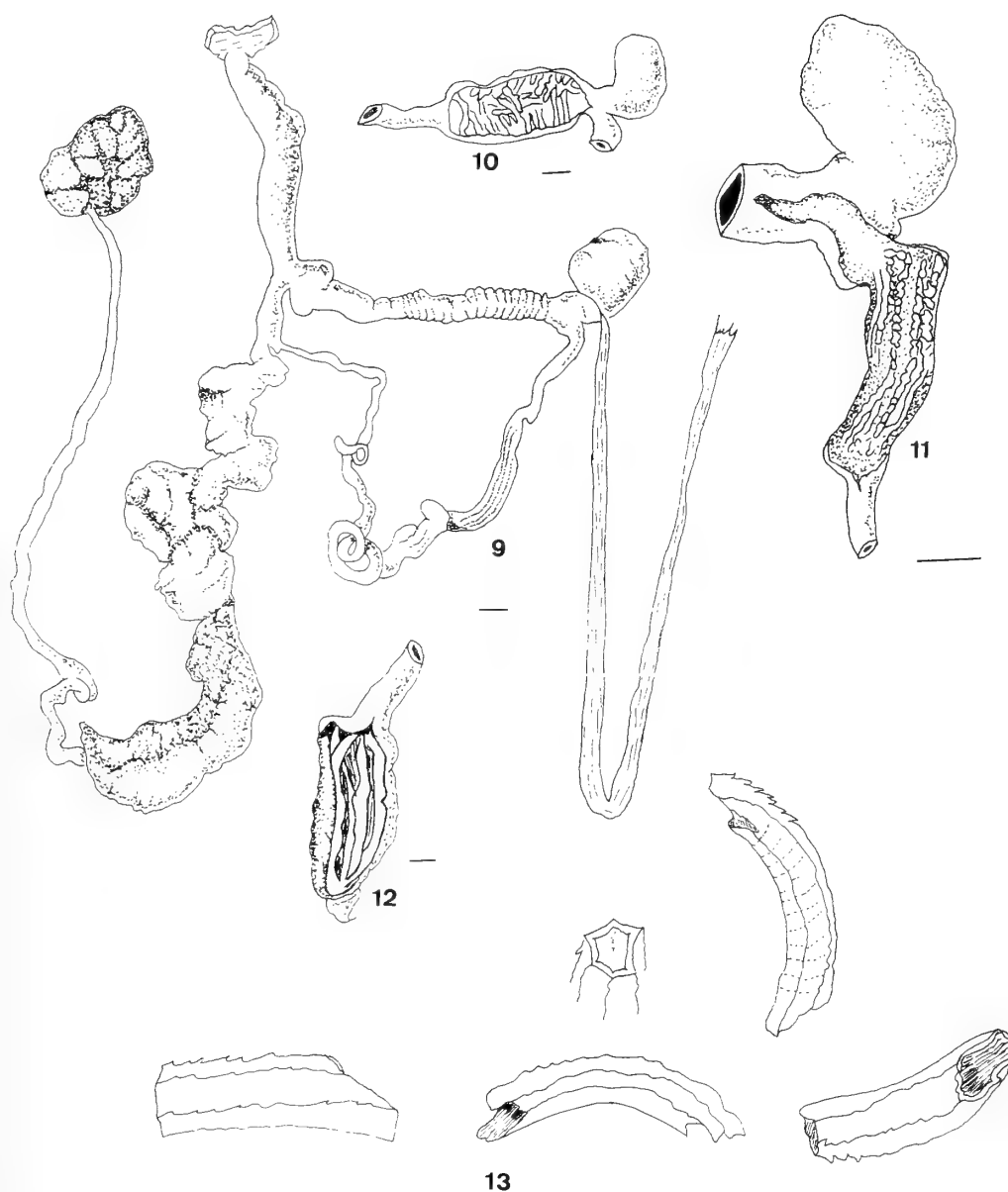
Material examined: Locations in Portugal (Figure 14): Sabugueiro (Serra da Estrela), 29TPE17, 28 March 1983, 23 specimens; Sao Romao (Serra da Estrela), 29TPE07, 29 March 1983, 1 specimen; Ermita de Nossa Senhora do Desterro (Serra da Estrela), 29TPE17, 29 March 1983, 14 specimens; Portela do Homem (Serra de Gerês), 29TNG72, 9 March 1984, 1 specimen; Albergaria (Serra

de Gerês), 29TNG72, 31 October 1984, 7 specimens; Curral de Leonte (Serra de Gerês), 29TNG72, 1 November 1984, 8 specimens; Quintás (Chaves), 29TPG10, 2 November 1984, 1 specimen; Chaos (Guarda, Serra da Estrela), 29TPE48, 28 November 1984, 14 specimens, and 29 November 1984, 2 specimens; Rabal (Bragança), 29TPG83, 6 December 1985, 41 specimens; Sao Pedro do Sul, 29TNF71, 9 December 1985, 1 specimen; Vouzela (Sao Pedro do Sul), 29TNF70, 10 December 1985, 16 specimens; Paços (Sao Pedro do Sul), 29TNF70, 10 December 1985, 1 specimen; Luso (Coimbra), 29TNE56, 11 December 1985, 2 specimens, and 28 January 1986, 1 specimen; Viana do Castelo, 29TNG11, 14 December 1985, 16 specimens; Mirador de Sao Silvestre (Viana do Castelo), 29TNG11, 15 December 1985, 3 specimens.



Explanation of Figures 4 to 8

Figures 4-8. *Geomalacus maculosus*. Figure 4. Organs *in situ*. Figure 5. Digestive tract. Figure 6. Ocular retractor muscles. Figure 7. Limacella. Figure 8. Dorsal view of pallial complex. Scale 1 mm.



Explanation of Figures 9 to 13

Figures 9–13. *Geomalacus maculosus*. Figure 9. Genital apparatus. Figure 10. Interior of intermediate canal. Figure 11. Interior of epiphallus. Figure 12. Interior of oviduct. Figure 13. Spermatophore. Scale 1 mm.

Description: *External morphology* (Figures 1–3): Large slug, 120 mm long maximum, though normally only 70–80 mm (*in vivo*); length in 70% alcohol 60–70 mm.

Body surface mottled white or yellow, for gray or green body color, respectively. Yellow mucus. White sole. In 70% alcohol, back yellowish green with some dark spots.

Juveniles sometimes have two longitudinal lateral bands disappearing with age.

Internal anatomy: (a) Digestive tract (Figure 5): Intestine with two circumvolutions.

(b) Limacella (Figure 7): Solid, with clear nucleus, long, irregular in outline and width, growth lines just visible.

(c) Genitalia (Figures 9–13): Atrium long, lined internally by a series of longitudinal grooves. Vaginal diverticulum very long, slightly dilated around the atrium and lined inside by circular grooves, thus appearing festooned externally.

Free oviduct short, covered inside by seven partially overlapping longitudinal grooves giving aspect of ligule.

Bursa copulatrix rounded, with short duct; retractor

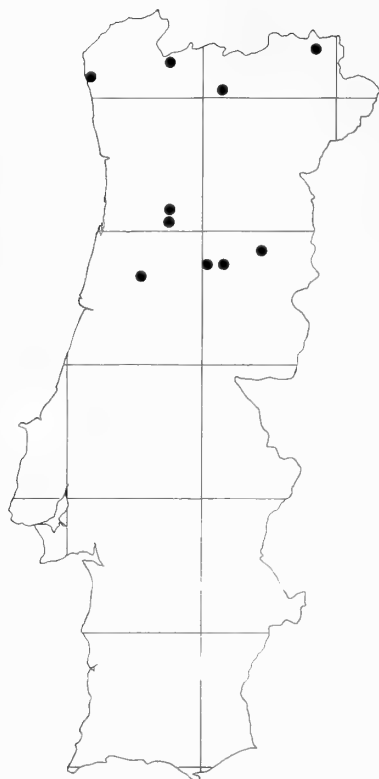


Figure 14

Provisional distribution of *Geomalacus maculosus* in Portugal.

muscle anchored inside, very long and inserting in caudal part of the animal, close to hermaphrodite gland.

Epiphallus (Figure 11) large, rolled spirally and lined internally by many perfectly aligned papillae giving the appearance of longitudinal grooves visible externally. Vas deferens thinner and smaller.

Ovotestis consists of dark colored groups of acini.

In only one of the studied specimens were fragments of spermatophore found (Figure 13), so we can not describe spermatophore morphology.

Habitats and distribution: The slug is crepuscular, disappearing during the day in gaps between rocks, in the earthy slopes, or under tree bark. This earthworm-like ability to hide in cracks is due to its flattened, uniformly wide body (only the lower part is slightly tapered) (PLATTS & SPEIGHT, 1988).

SIMROTH (1891) recorded two characteristics of this species: one, the strange way that it curls when eating, such that the head and eyes protrude only slightly from beneath the mantle, and, the other, its reaction when caught, in which the lower part of the sole folds up to the upper part.

Geomalacus maculosus can live on feeds supplemented with pieces of fungi and fresh vegetables (PLATTS & SPEIGHT, 1988). It does not seem to require a particular diet since it has been found to eat a wide variety of lichens

and liverworts (TAYLOR, 1907). In Portugal we captured *G. maculosus* browsing on lichens growing on granite and similar rocks, on walls surrounding fields, in cemeteries and on church walls; on some occasions it was found on schists, or greywackes (Brangança), red sandstones, conglomerates, or marls (Luso-Buçaco). In woods we found it on the mossy or lichen-covered barks of *Quercus robur*, *Q. suber*, *Q. lusitanica*, *Castanea sativa*, or *Pinus pinaster*.

All the zones where it has been found have Atlantic climates, above 1000 mm mean annual precipitation and a mean annual temperature varying between 8°C in upland regions and 12°C in lowland. This species is common to all of northern Portugal down to the Mondego River and the Serra da Estrela. Its distribution is restricted to the Atlantic area of the Iberian Peninsula (north Portugal, Galicia, Asturias, and Santander) and the south of Ireland. It has been reported from Brittany, France, but we would not collect it there and thus its presence in France remains unconfirmed.

PLATTS & SPEIGHT (1988) recommended the need to protect *Geomalacus maculosus* in Ireland, where it is a rare species. With regards to the fauna of northern Spain and Portugal, the species is fairly common and we collected many specimens in Santander, Asturias, León, Galicia, and the north of Portugal, finding, as did Platts & Speight, that the global distribution of this genus is restricted to the Lusitanian area.

Discussion: In his description of *Geomalacus grandis* SIMROTH (1893) said that it is closely related to *G. maculosus*. In a synoptic table he noted the characteristics of the four species found in Portugal, showing that the only differences between *G. maculosus* and *G. grandis* are the size of the atrium and the length of the animal (in both cases *G. grandis* is bigger). It is a possible that the specimens of *G. maculosus* Simroth studied from Ireland were juveniles, which would explain his assignment of 40 specimens collected at the Serra de Gerês to *G. maculosus* and the assignment two years later of sexually mature individuals to *G. grandis*.

We had the opportunity of studying a topotype of *Geomalacus maculosus* deposited in the British Museum (London), the external and internal anatomy of which coincide with the specimens we collected in northern Portugal. From this determination we are able to definitively synonymize *G. grandis* and *G. maculosus*.

Geomalacus anguiformis (Morelet, 1845)

(Figures 15–23)

Limax anguiformis Morelet, 1845

Limax squammantinus Morelet, 1845

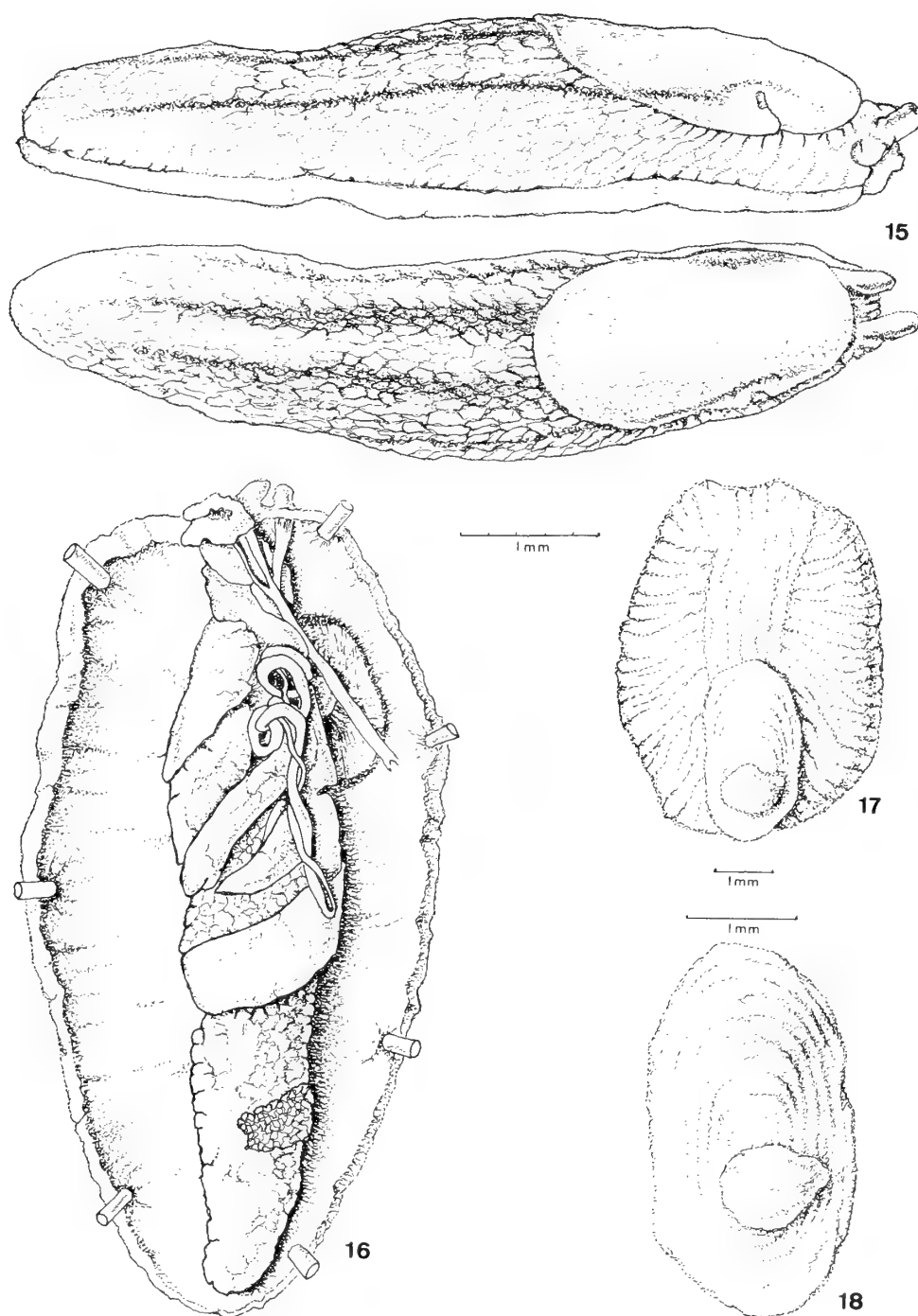
?*Limax viridis* Morelet, 1845

Geomalacus anguiformis (Morelet, 1845): POLLONERA, 1890

Geomalacus squammantinus (Morelet, 1845): POLLONERA, 1890

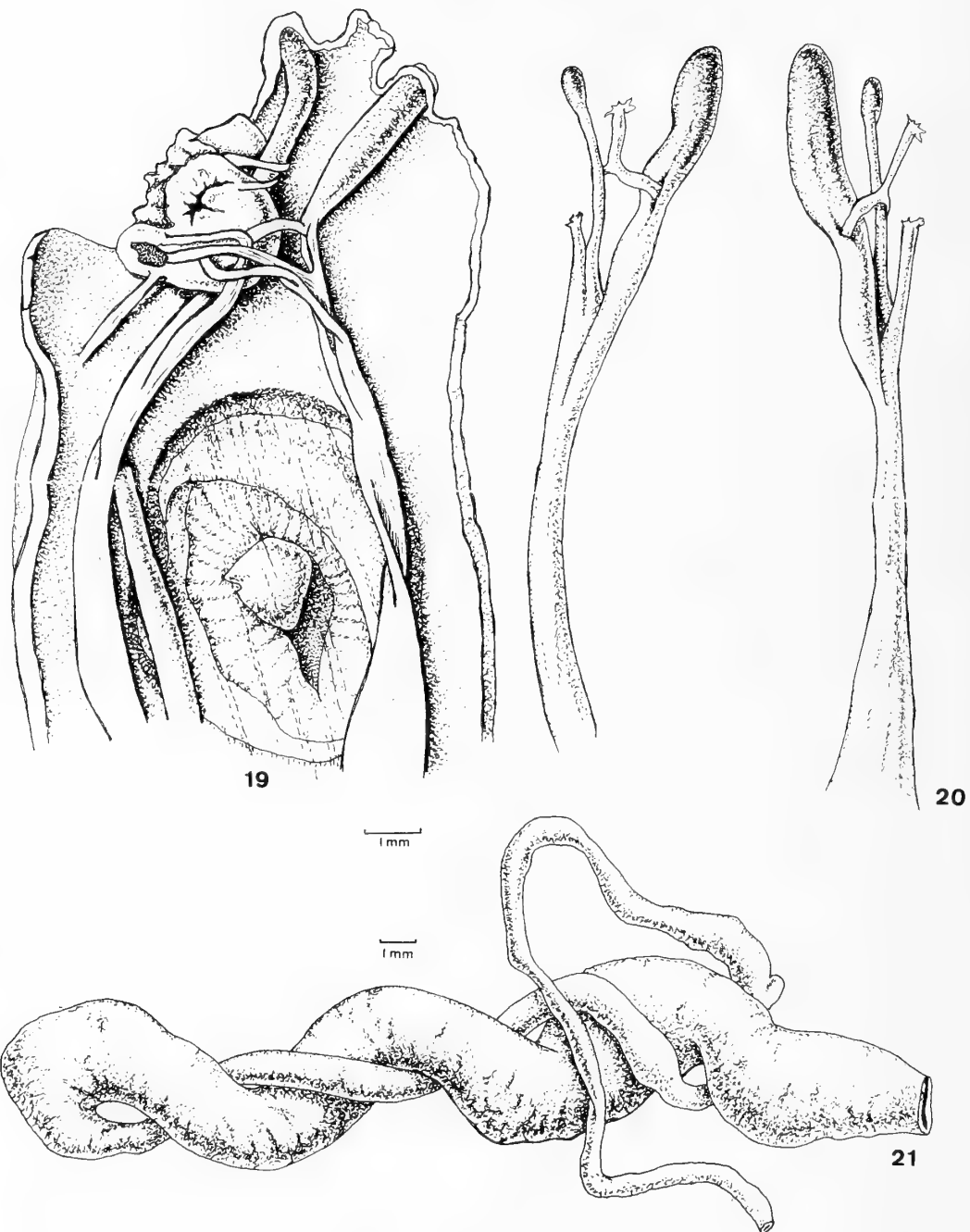
Geomalacus anguiformis (Morelet, 1845): SIMROTH, 1891

Geomalacus anguiformis (Morelet, 1845): NOBRE, 1941



Explanation of Figures 15 to 18

Figures 15–18. *Geomalacus anguiformis*. Figure 15. Lateral and dorsal views of a specimen from the Serra de Monchique (type locality of *Geomalacus anguiformis*). Figure 16. Organs *in situ*. Figure 17. Dorsal view of pallial complex. Figure 18. Limacella. Scale 1 mm.



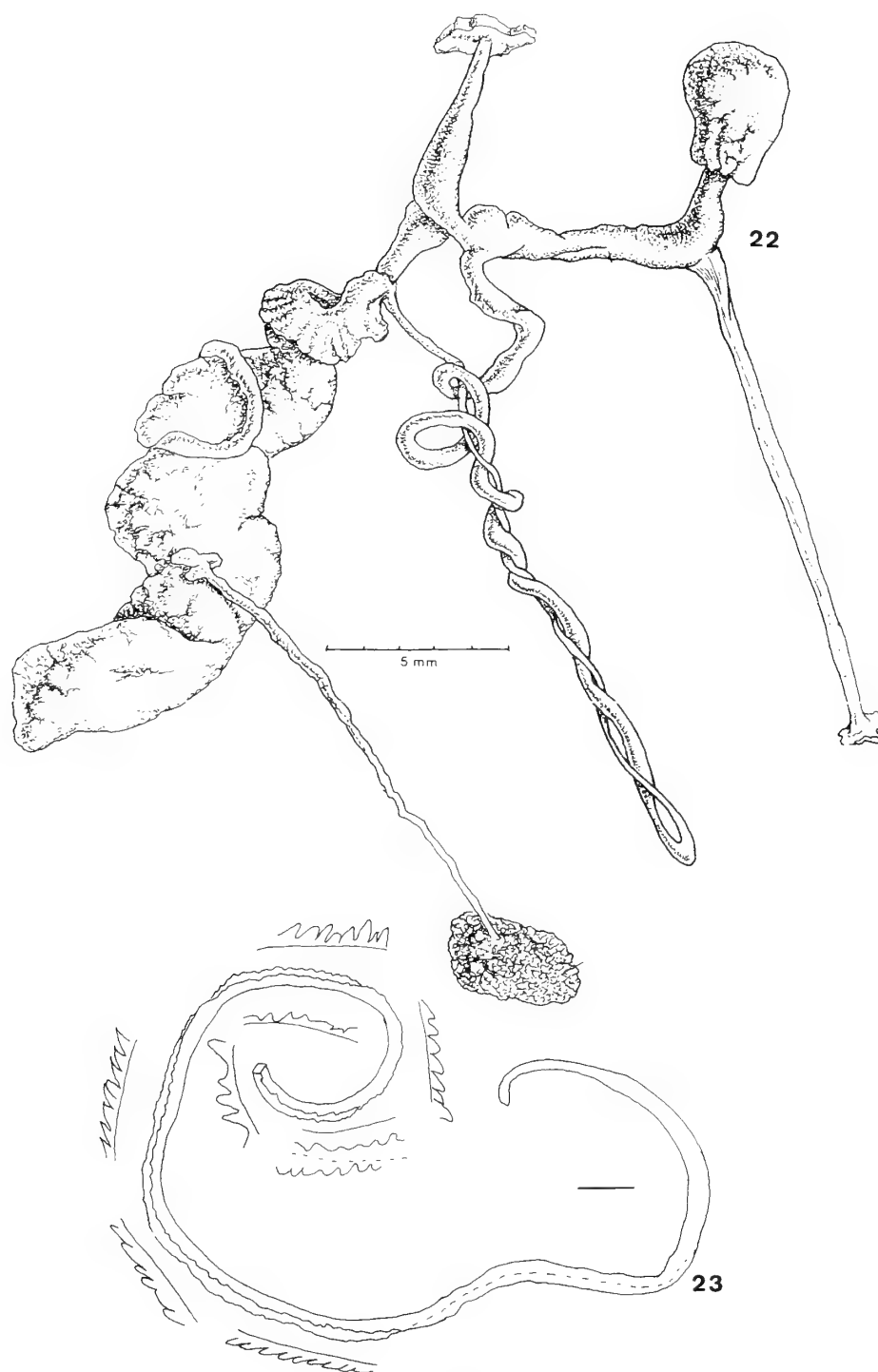
Explanation of Figures 19 to 21

Figures 19–21. *Geomalacus anguiformis*. Figure 19. Pallial complex. Figure 20. Ocular retractor muscles. Figure 21. Digestive tract. Scale 1 mm.

Description and iconography: *Geomalacus anguiformis* SIMROTH, 1891: 355; pl. 5, fig. 7; pl. 6, fig. 8; pl. 7, figs. 2–2b.

Material examined: Locations in Portugal (Figure 24): Marmeleite (Serra de Monchique), 29SNB23, 15 April 1984, 17 specimens; Caldas de Monchique (Serra de

Monchique), 29SNB32, 15 April 1984, 19 specimens; Alferce (Serra de Monchique), 29SNB43, 16 April 1984, 20 specimens; Monchique, 29SNB33, 16 April 1984, 15 specimens, and 2 December 1984, 12 specimens; Road Monchique-Foia, 29SNB32, 16 April 1984, 3 specimens; Barranco do Velho (Serra do Caldeirao), 29SNB92, 30 November 1984, 24 specimens, and 1 December 1984, 8



Explanation of Figures 22 and 23

Figures 22, 23. *Geomalacus anguiformis*. Figure 22. Genital apparatus. Figure 23. Spermatophore (with the teeth enlarged). Scale 1 mm.



Figure 24

Provisional distribution of *Geomalacus anguiformis* in mainland Portugal.

specimens; Alportel (Serra do Caldeirao), 29SNB91, 1 December 1984, 52 specimens, and 2 December 1984, 8 specimens.

Description: *External morphology* (Figure 15): Extended length 60–70 mm, not exceeding 50 mm in 70% alcohol.

Body coloring very varied. Young juveniles blue-black with whitish tubercles; back with almost black bands; juveniles somewhat lighter, blue more prominent, masking the white of the dorsal tubercles, while bands broaden; adults chestnut color, yellow at body margins, the four dorsal bands dark chestnut, in some cases almost black; some specimens gray with black bands.

Back grayish-brown in 70% alcohol, with four dark longitudinal bands; the two central bands reaching the shield. Sole whitish, lateral margins light.

Internal anatomy: (a) Digestive tract (Figure 21): Intestine with two circumvolutions.

(b) Limacella (Figures 17, 18): Oval, with inferior nucleus and light growth lines.

(c) Genitalia (Figures 22, 23): Genital atrium large and cylindrical, in adults covered externally by glandular mass, in juveniles unmarked, lined internally by 7 to 12 rectangular longitudinal grooves in both. Vaginal diverticulum short, cylindrical or spherical, smooth, with little internal grooving (papillous folds).

Bursa copulatrix oval, bursa copulatrix duct very long,

entering, along with the epiphallus, in the vaginal diverticulum. Bursa retractor muscle long, connected at lower third of duct; folds into U- or L-shape where it enters duct.

Free oviduct smaller than the genital atrium. Epiphallus tubular, dilated apically, 10–15 times larger than the oviduct, covered inside with serrated helicoidal or longitudinal grooving. Vas deferens shorter (by almost half) than the epiphallus. Epiphallus-vas deferens transition is indistinct.

Spermoviduct well developed. Albumin gland large and whitish. Hermaphrodite gland long and slightly festooned. Ovotestis spherical, with darkish acini.

Spermatophore (Figure 23) long, approximately 35 mm, square in cross section and provided with three longitudinal rows of non-helicoidal toothlets. Amber in color, lacking a set of teeth at one end.

Habitats and distribution: In Portugal, *Geomalacus anguiformis* occurs in areas of clayey schists, greywackes, and sandstones (Serra do Caldeirao) and on medium- to coarse-grained nepheline-syenites (Serra de Monchique). In both sierras, species of the genus *Quercus* dominate together with *Olea oleaster*, *Pinus* sp., *Rhododendron ponticum*, and *Arbutus unedo*.

The Serra de Monchique exhibits a thermoatlantic climate—i.e., always humid, sub-Mediterranean mesothermic oceanic climate. In the Serra do Caldeirao the climate is Mediterranean. In both sierras, mean annual rainfall is about 1000 mm and the mean annual temperature about 16°C (ANONYMOUS, 1984). These sierras, especially the Serra de Monchique, represent the only green, humid zones in all the Portuguese Algarve.

Although *Geomalacus anguiformis* is known only in the south of Portugal, it is very likely that it also occurs in the Spanish provinces of Badajoz and Huelva. As a species it is confined to the southeast of the Lusitanian area and found, at the moment, in the mountain chains of southern Portugal.

Discussion: The specimens we collected show great variation as regards color. This may be diet related, since the young juveniles and the juveniles were collected in the spring browsing on lichens on rocks (granite and schist), while adults, captured in the autumn, were feeding on toadstools in the woods of both sierras, consisting mostly of cork oak (*Quercus suber*) and *Arbutus unedo*.

A comparison of our specimens with those sketched by SIMROTH (1891:pl. 3, fig. 8) revealed that the festoonery shown by this author on the vaginal diverticulum and in the bursa copulatrix duct are not found on any of the specimens we have dissected. This difference may be due to the method of preserving the animals, since Simroth himself stated that in November 1891 he collected 20 specimens of *Geomalacus anguiformis* on fungi in the Serra de Monchique and transported them alive to Lisbon, except for five specimens that he preserved in alcohol; it is possible that these specimens were already almost dead before being placed in alcohol.

One of the specific names that we have synonymized is

Limax viridis Morelet, 1845. The original description of this species stated that *L. viridis* has a blunted cowl on its back. This cowl is not characteristic of the Arionidae, and after considering the opinions of other authors such as POLLONERA (1890) and SIMROTH (1891) on *Geomalacus anguiformis*, the synonymy is in doubt, as indicated with a question mark.

Geomalacus oliveirae Simroth, 1891, is closely related to *G. anguiformis*. It differs externally in that it is shorter. This difference is also seen in the genitalia, apart from the oviduct, which is slightly larger in *G. oliveirae* than in *G. anguiformis*. *Geomalacus oliveirae* was described from the Serra da Estrela (central-north Portugal) and *G. anguiformis* was described from the two sierras of south Portugal. We have not captured any specimens of either species in the region between the southern and northern mountain chains. After comparing their genitals, finding that they are different, and confirming their geographical isolation, we consider that both species are distinct.

Recently, WIKTOR & PAREJO (1989) redescribed *Geomalacus anguiformis* with specimens collected in the province of Toledo (Spain). Their description does not agree with that of the *G. anguiformis* we collected in the Serra do Caldeirao and the Serra de Monchique (the type locations for *G. anguiformis*), but it is in keeping with the specimens we captured in the Serra da Estrela and assigned to *G. oliveirae*. The taxonomic position of the species redescribed by Wiktor & Parejo is discussed at a later point.

Geomalacus oliveirae Simroth, 1891

(Figures 25–31)

Description and iconography: *Geomalacus oliveirae* SIMROTH, 1891:359; pl. 6, fig. 9.

Material studied: Locations in Portugal (Figure 32): Guarda, 29TPE48, 28 March 1983, 1 specimen; Caldas de Manteigas, 29TPE27, 28 March 1983, 1 specimen; Chaos, 29TPE48, 28 November 1984, 5 specimens; Sameiro, 29TPE27, 29 November 1984, 1 specimen; cross-roads of Guarda-Manteigas with Gouveia, 29TPE17, 29 November 1984, 1 specimen.

Description: *External morphology* (Figures 25, 26): *In vivo* length does not exceed 45 mm, 30 mm in alcohol. Body is chestnut in color with four black bands. Body margins light colored. The two internal bands not totally continuous, interrupted at irregular intervals in most individuals. Sole white, tripartite with very narrow central zone.

In 70% alcohol, body grayish-brown, with two darker longitudinal bands on either side of two other bands, also dark. Light lateral margins of body; sole whitish.

Internal anatomy: (a) Digestive tract (Figure 27): Characteristic of the genus.

(b) Limacella (Figure 28): Oval, with light inferior nucleus. Growth lines also light colored.

(c) Genitalia (Figures 29–31): Genital atrium cylindrical, covered externally by a glandular mass only in adults,

internally 7–9 longitudinal grooves. Vaginal diverticulum short and smooth.

Bursa copulatrix rounded, with short, thick duct; covered internally by a series of transverse grooves festooned with a paving-like design. Bursa and duct darkish. Before junction with epiphallus, the bursa copulatrix duct has an annular dilation covered internally by short, thick longitudinal grooves.

Oviduct cylindrical, somewhat larger than atrium, lined with fine longitudinal grooves. Forms continuation of atrium.

Epiphallus cylindrical, slightly larger than vas deferens, lined with 7–9 longitudinal, festooned grooves.

Retractor muscle enters close to bursa copulatrix.

No spermatophore found.

Spermoviduct well developed. Albumin gland whitish. Hermaphroditic duct lengthened and festooned. Ootestis spherical, with darkish acini.

Habitats and distribution: The area of Portugal where this species was found is granitic, with Mediterranean-type vegetation below 1300 m and *Betula pubescens*, *Pinus sylvestris*, and *Juniperus communis* above. A change with elevation is also seen in the climate, which above 1300 m is very wet, cold in winter, and warm in summer. The mean annual precipitation exceeds 2400 mm and the mean temperature is between 7.5 and 10°C.

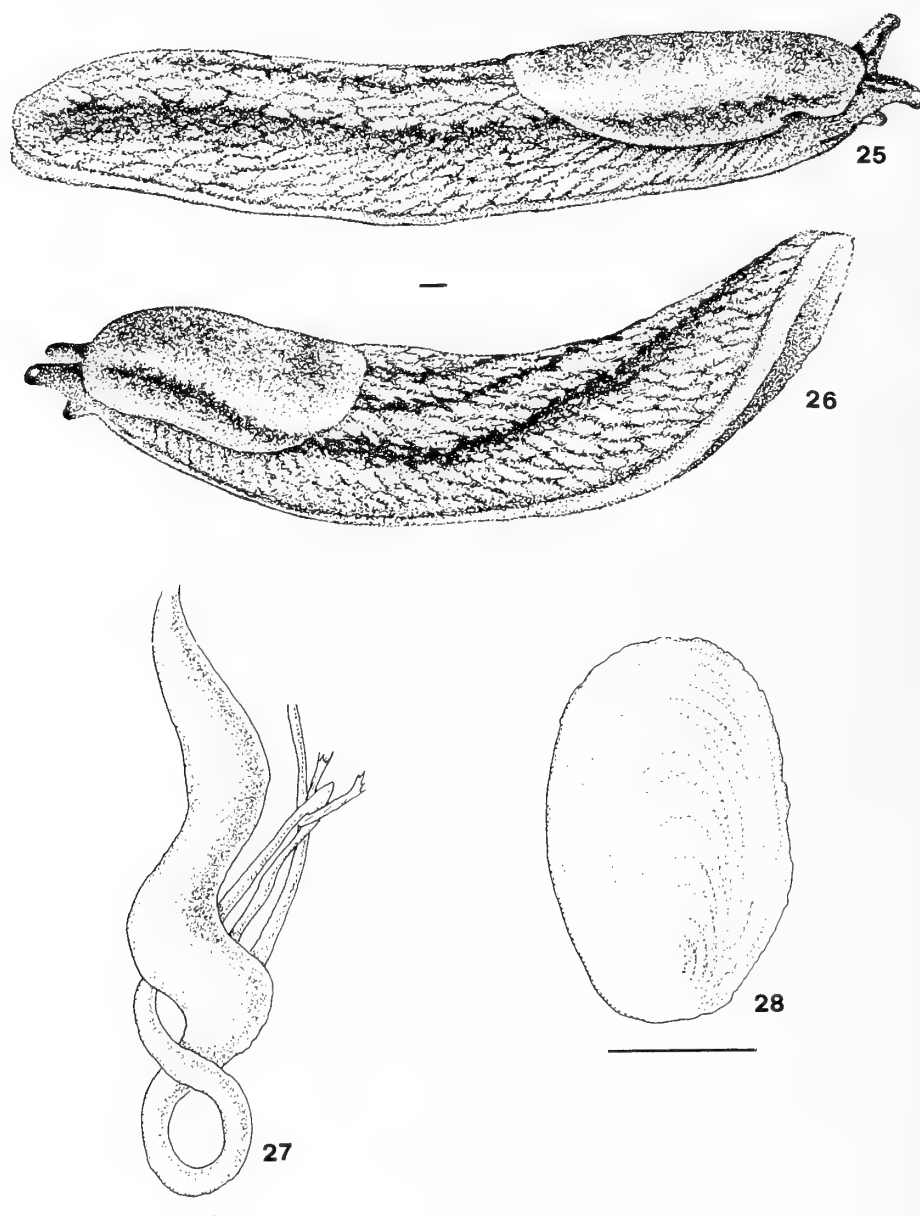
Discussion: The species is virtually unknown, since the only description is from 1891. Since then, it has been overlooked, not taken into account, or considered a synonym of *Geomalacus anguiformis*, a close species which differs in some respects, however.

SIMROTH (1893) contrasted their characteristics in a table similar to the following:

	<i>G. oliveirae</i>	<i>G. anguiformis</i>
Atrium	long	long
Atrium-penis	lateral; short	to the end of atrium; medium
Bursa duct	long	long
Receptaculum	rounded	stretched out
Proximal insertion of retractor	close to the lung	close to the posterior end of the body
Distal insertion	close to the bursa	in the bursa duct

We noticed the following differences:

	<i>G. oliveirae</i>	<i>G. anguiformis</i>
Atrium	lengthened; pigmented 7–9 longitudinal internal grooves	lengthened; pigmented 9–10 longitudinal internal grooves
Vaginal diverticulum	smooth or with light nervations	7 thick grooves



Explanation of Figures 25 to 28

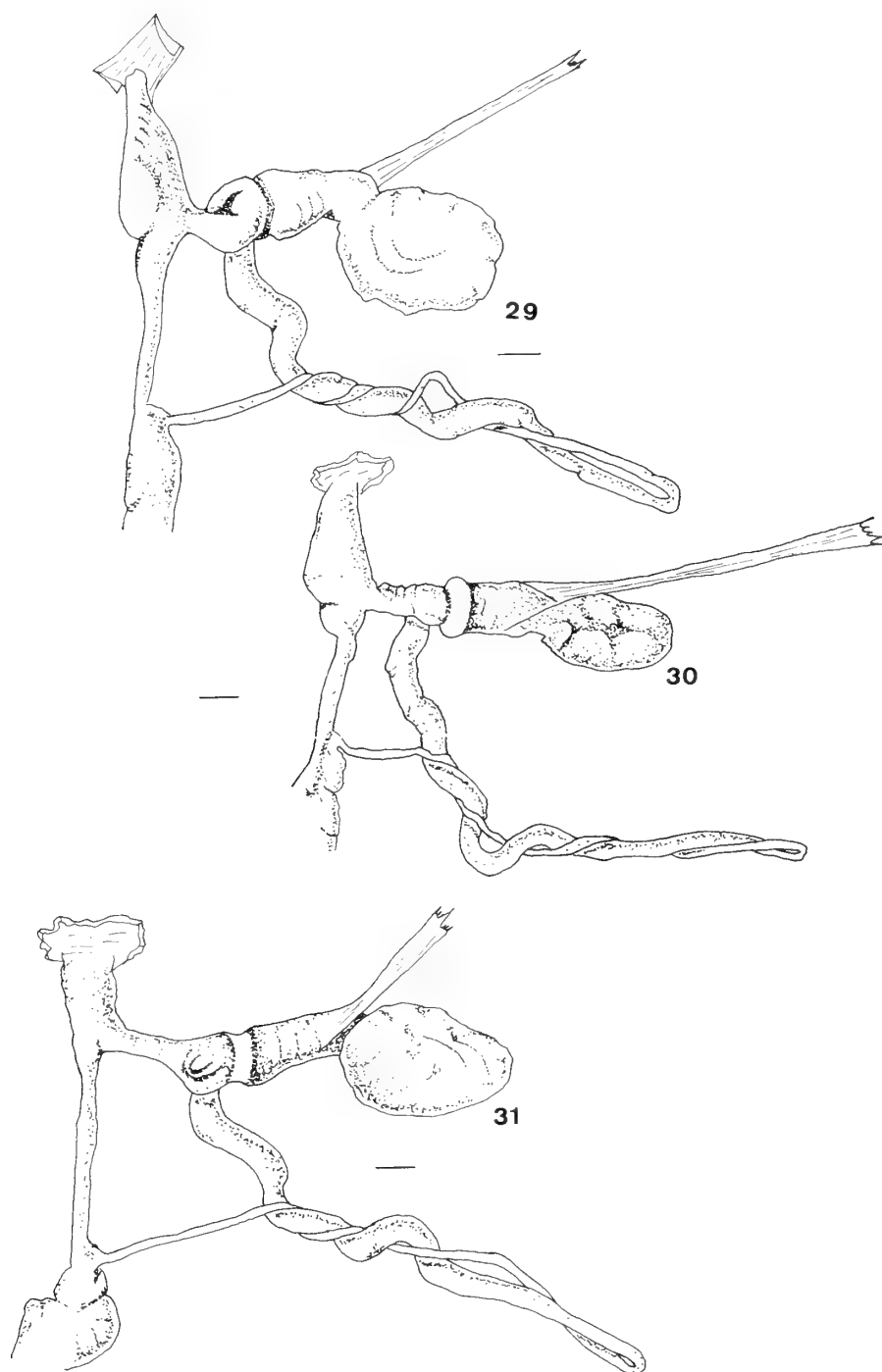
Figures 25-28. *Geomalacus oliveirae*. Figures 25, 26. Dorsal and lateral view of a specimen from the Serra da Estrela (type locality of *Geomalacus oliveirae*). Figure 27. Digestive tract. Figure 28. Limacella. Scale 1 mm.

Bursa duct	short and pigmented around the bursa	large, twisted into an L-shape
Oviduct	large	short
Muscle	close to the bursa	further away
Epiphallus + vas deferens	30-35 mm	50-60 mm
Bursa	pigmented	not pigmented

The differences between the two species, although few, are constant, leading us to think that these species could

be completely separate; to their anatomical distinctness we should add differences in vegetation, soil, and climate, along with a real geographical separation, since we have not captured any representatives of either species, nor any intermediate form in between the two southern ranges (Caldeirao and Monchique) and the northern (Serra da Estrela).

As regards climate, the Serra da Estrela has a mean annual precipitation exceeding 2400 mm and a mean annual temperature of below 10°C, compared to the 1000



Explanation of Figures 29 to 31

Figures 29–31. *Geomalacus oliveirae*. Genital apparatus of three specimens from the Serra da Estrela. Scale 1 mm.

mm and 16°C of the sierras of Caldeirao and Monchique. As regards the vegetation of the two sierras in the south (Caldeirao and Monchique) dominant species belong to the genus *Quercus* (*Q. faginea*, *Q. lusitanica*, *Q. suber*, *Q. ilex*) together with *Olea oleaster* and *Pinus pinea*; in the

Serra da Estrela we find *Betula pubescens*, *Castanea sativa*, *Juniperus communis*, *Pinus silvestris*, and *Quercus pyrenaica*. In the Serra da Estrela the soil contains high levels of aluminum, carbon, and nitrogen and low levels of magnesium, potassium, calcium, and sodium, while the soils

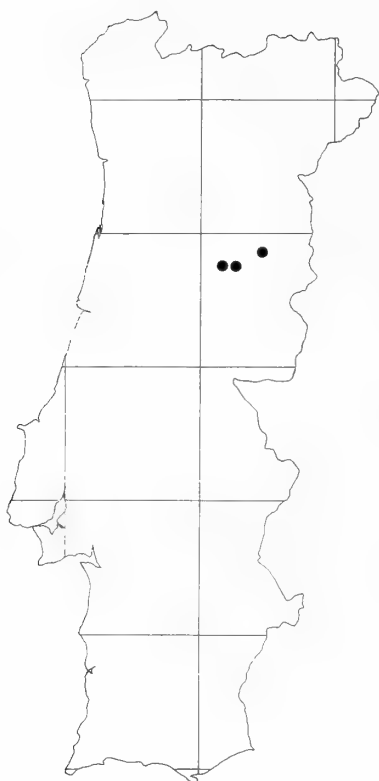


Figure 32

Provisional distribution of *Geomalacus oliveirae* in mainland Portugal.

of the two southern sierras have high levels of magnesium, potassium, sodium, and calcium and low levels of aluminum, carbon, and nitrogen.

Curiously, the light pigmentation that appears in the bursa duct, the bursa, and the atrium of *Geomalacus oliveirae* also appeared in the species of the genus *Arion* that we found in the Serra da Estrela.

As already stated, WIKTOR & PAREJO (1989) have re-described *Geomalacus anguiformis* with specimens collected in the province of Toledo (Spain). These specimens are of the same size as *G. oliveirae*; the bursa copulatrix duct is short, as is the retractor muscle; and the epiphallus and vas deferens together, in both cases, do not exceed 35 mm in length. In contrast, as already mentioned in the discussion of *G. anguiformis*, the specimens of the Serra do Caldeirao and Serra de Monchique have a large bursa copulatrix duct, folded into an L-shape, and the retractor muscle is just as long, entering at the caudal part of the animal; furthermore, the epiphallus and vas deferens are, together, twice as long as those found in *G. oliveirae*, exceeding 60 mm in most of the specimens dissected.

From all that has been said, we believe that the report from Toledo corresponds to *Geomalacus oliveirae* and not to *G. anguiformis*, which represents the first sighting of *G. oliveirae* for Spain. But this will only be confirmed when

the Iberian Peninsula is sampled systematically from the center down, to see whether there is continuity in the distribution of these two species in the sierras of the center and south of the peninsula.

ACKNOWLEDGMENTS

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The Taxonomic Status of *Buccinanops* d'Orbigny, 1841 (Gastropoda: Nassariidae)

by

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Abstract. The radulae of *Buccinanops cochlidium* (Dillwyn, 1817) and *B. moniliferum* (Kiener, 1834) were observed for the first time using the scanning electron microscope. Radular, morphological, and reproductive characters of the genera *Bullia*, *Dorsanum*, and *Buccinanops* are compared. It is concluded that the South American species belong to the genus *Buccinanops*.

INTRODUCTION

Species of the genus *Buccinanops* d'Orbigny, 1841, have been considered as belonging to several different taxa in previous works. Table 1 shows the genera and subgenera to which these species have been assigned by previous authors.

Seven species are presently included in the genus *Buccinanops*, all of them endemic to South America (see Table 2). Members of *Buccinanops* live in soft bottomed, shallow waters of the intertidal or infralittoral zones. They generally live in dense groups, and most of the species are scavengers.

The aim of this paper is to reinstate *Buccinanops* to full generic status within the family Nassariidae. It was compared with *Bullia* Gray in GRIFFITH & PIDGEON, 1834, and with *Dorsanum* Gray, 1847, because they are similar in shell morphology. Radular, morphological, conchological, and reproductive features were used for this comparison.

MATERIALS AND METHODS

Radular studies were carried out on two species of *Buccinanops*: *B. cochlidium* from the localities detailed in Table 3, and *B. moniliferum* from Praia de Pereque (Guaruja, Sao Paulo, Brazil). The radulae of both species were treated following the method of SOLEM (1972) and observed under the SEM in the Museo de Ciencias Naturales, La Plata, Argentina (MLP). Specimens of all species of *Buccinanops* were also used from the malacological collection housed in the División Zoología Invertebrados (MLP).

RESULTS

Radula

Buccinanops cochlidium has a rachiglossan radula (Figures 4–6). The central tooth is multicuspidate with 5–11 cusps that increase in size towards the middle of the series. The rachidian base is strongly curved when compared to the other species of the genus.

The inner and outer cusps of the lateral teeth are hook-shaped. The first cusp may be bifid (Figure 4). The lateral teeth always have 1–3 intermediate cusps. Generally, the lateral teeth are symmetrical, but in some cases there is a peculiar asymmetry in the number and shape of cusps (Figure 4).

The number of cusps (5–11) in the rachidian teeth of *Buccinanops cochlidium* represents the main variation. In addition, one or two prominent central cusps were also observed. There is no relation between the number of cusps, age, and sex (see Table 3).

The radula of *Buccinanops moniliferum* is similar to that of *B. cochlidium* (Figures 1–3). The central tooth has 11 cusps that decrease in size towards the sides. The rachidian base is gently concave with sharp borders. A more conspicuous central cusp may be present. The lateral teeth have two hooked cusps with 1–4 intermediate cusps.

Operculum

Operculum morphology in all *Buccinanops* species is very uniform. The operculum is large, sub-oval, and smooth margined, and has a subterminal nucleus. The growth lines are well defined.

Table 1

Genera and subgenera in which South American species of *Buccinanops* were placed by previous authors.

Buccinanops	Bullia (Buccinanops)
COSSMANN (1901)	ADAMS & ADAMS (1853)
STREBEL (1906)	CHENU (1859)
PEILE (1937)	TRYON (1882)
CARCELLES & PARODIZ (1939)	THIELE (1929)
CARCELLES (1944, 1950)	CERNOHORSKY (1982)
CARCELLES & WILLIAMSON (1951)	ALLMON (1990)
BARATTINI & URETA (1960)	
KLAPPENBACH (1961)	Dorsanum
CASTELLANOS (1970)	COSSMANN (1901)
RIOS (1970, 1975)	CARCELLES & PARODIZ (1939)
SCARABINO (1977)	CARCELLES (1944)
CERNOHORSKY (1984)	BARATTINI & URETA (1960)
RIOS (1985)	CASTELLANOS (1970)
CALVO (1987)	RIOS (1970, 1975)
	SCARABINO (1977)
Buccinum	Buccinanops (Dorsanum)
DILLWYN (1817)	RIOS (1985) (only for <i>B. moniliferum</i>)
KING & BRODERIP (1832)	
KIENER (1834)	
D'ORBIGNY (1841)	
DESHAYES in DESHAYES & EDWARDS (1844)	
Bullia	
REEVE (1846–1847)	
PILSBRY (1897)	
IHERING (1907)	
CERNOHORSKY (1982)	
ABBOTT & DANCE (1983, 1986)	

Shell

In general, the shell is large and thick, with an oblique plait at the base and a carina behind the fasciole. It lacks ornamentation except for growth lines; however, some species have sharp tubercles on the subsutural shoulder of the last whorls (*Buccinanops moniliferum* (Kiener)), subsutural spiral lines (*B. uruguayense* (Pilsbry)), or axial ribs on the first three or four teleoconch whorls (*B. cochlidium* (Dillwyn)). The apex is large, short, and blunt.

Egg Capsules

The egg capsules of all known species of *Buccinanops* show the same morphological pattern (PENCHASZADEH, 1971a, b, 1973). The capsules are attached to the callus and adjacent area of the mother's shell by means of a short pedicle. More than 80 capsules are attached to several specimens of *B. cochlidium*. The capsules, which are oval, flattened, and clear, vary in size, form, and ornamentation according to the species.

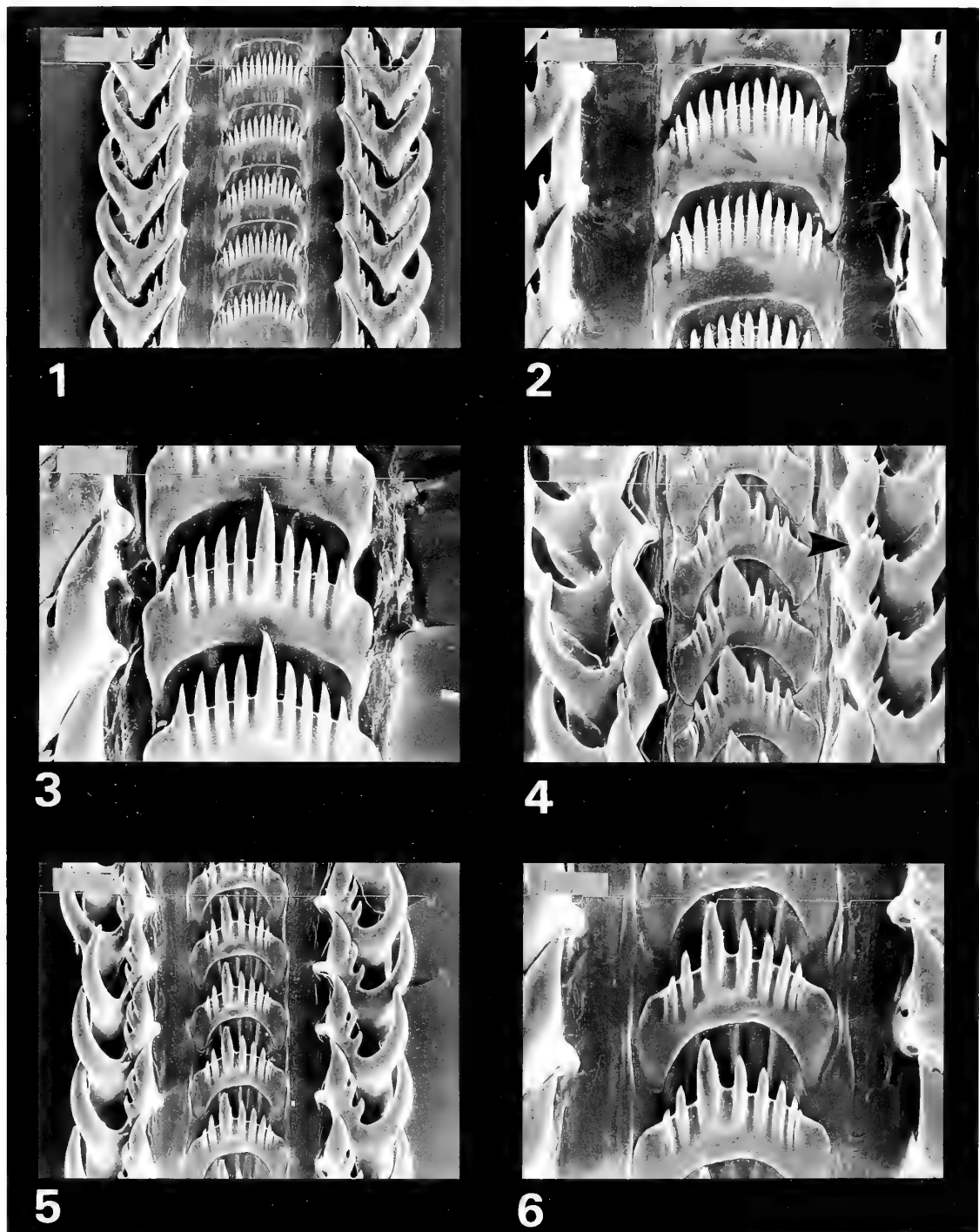
Table 2

Recent species of *Buccinanops* d'Orbigny, 1841. Institutional abbreviations: ZMC—Zoological Museum, Copenhagen, Denmark; BM—British Museum (Natural History), London, England; MHNG—Muséum d'Histoire Naturelle, Geneva, Switzerland; MN—Museo Nacional de Historia Natural, Montevideo, Uruguay; ANSP—Academy of Natural Sciences, Philadelphia, USA.

Species and author	Year	Type locality and repository
<i>B. cochlidium</i> (Dillwyn)*	1817	Islands of South Seas. ZMC
<i>B. deforme</i> (King & Broderip)	1832	Gorriti, Argentina. BM1985003
<i>B. moniliferum</i> (Kiener)	1834	Terra Nova [sic]. ?
<i>B. paytense</i> (Kiener)†	1834	Payta, Peru. ?
<i>B. globulosum</i> (Kiener)	1834	?. MHNG1296/17/1
<i>B. uruguayense</i> (Pilsbry)	1897	Maldonado Bay, Uruguay. ANSP70504
<i>B. duartei</i> Klappenbach	1961	La Coronilla, Uruguay. MN0709

* = *B. gradatum* (Deshayes in Deshayes & Edwards, 1844).

† = *B. squalidum* King & Broderip, 1832, non Gmelin, 1791.



Explanation of Figures 1 to 6

Figures 1–6. Genus *Buccinanops*. Scanning electron micrographs of radulae. Figure 1. *B. moniliferum*, general view; scale bar = 500 μm . Figure 2. Detail of rachidian teeth of the specimen in Figure 1; scale bar = 100 μm . Figure 3. *B. moniliferum*, detail of rachidian teeth; scale bar = 500 μm . Figure 4. *B. cochlidium*, arrowhead bifid cusps of the lateral tooth in asymmetric position; scale bar = 500 μm . Figure 5. *B. cochlidium*, general view; scale bar = 500 μm . Figure 6. *B. cochlidium*, detail of rachidian teeth; scale bar = 100 μm .

Table 3

Radular and opercular parameters of *Buccinanops cochlidium* (Dillwyn, 1817).

Shell length (mm)	Operculum length (mm)	Rachidian cusps	Lateral cusps	Sex	Locality
78	23.3	9	5	F	Pto. Piramide, Chubut
68.7	21.7	8	5	F	Pto. Piramide, Chubut
90.8	30	7	4	F	Pto. Piramide, Chubut
49	16.6	11	5-4	F	Pto. Piramide, Chubut
91	29	8	4	F	Rawson, Chubut
60.3	18.4	6	4	F	Rawson, Chubut
59.2	21.6	6	5-4	M	Rawson, Chubut
78.8	28.5	8	5	F	Mar del Plata, Buenos Aires
73.3	26	9	4	F	Mar del Plata, Buenos Aires
63.2	24.3	9	4	F	Mar del Plata, Buenos Aires
79.2	26	5	4	F	Mar del Plata, Buenos Aires
48.6	16	6	4	M	Pto. Piramide, Chubut
56	19	8	4	F	Pto. Piramide, Chubut
47	15.5	7	4	M	Pto. Piramide, Chubut
25.4	7.8	7	4	M	Pto. Piramide, Chubut
48.8	15.2	6	4	F	Pto. Piramide, Chubut
45.3	14.9	7	4	M	Pto. Piramide, Chubut
25	8.3	7	4	F	Pto. Piramide, Chubut
15.4	4.6	9	4	F	Pto. Piramide, Chubut

Larval Development

Buccinanops species with known larval development have one to nine embryos (*B. cochlidium*) that hatch in the crawling stage. However, each capsule may have up to 1600 nurse eggs (PENCHASZADEH, 1971a, b, 1973).

DISCUSSION

Despite minor specific differences among Recent species of *Buccinanops*, they form a very homogeneous group. In

contrast, the species of *Bullia* form a very heterogeneous one (ALLMON, 1990). *Dorsanum*, represented today only by *D. miran* (Bruguère) (sensu ALLMON, 1990), shows a very different set of features. Table 4 shows characteristic features of the three genera.

The radulae characteristic of the three genera differ. According to PEILE (1937), ADAM & KNUDSEN (1985), CALVO (1987), CERNOHORSKY (1984), and ALLMON (1990), rachidian teeth in *Bullia* and *Buccinanops* have similar morphology. *Buccinanops*, however, presents cusps that

Table 4

Comparison of generic features among *Buccinanops*, *Dorsanum*, and *Bullia*.

	<i>Buccinanops</i>	<i>Dorsanum</i>	<i>Bullia</i>
Shell	Large, with the base of the columella with one oblique plait; large and blunt apex	Medium to small size siphonal channel bordered by two spiral ridges; small and multispiral apex	Medium to small size, more slender; without periostracum; acute apex
Animal	Very large, with one posterior metapodial tentacle, without eyes, long cephalic tentacles	Medium in size without posterior metapodial tentacles, with eyes, short cephalic tentacles	Very large, with two posterior metapodial tentacles, without eyes, long cephalic tentacles
Operculum	Large, always without serrations, subterminal nucleus	Small, with smooth margins	Small, some with marginal serrations
Larval development	Young hatch as crawling veliger, only 1-9 eggs develop, others used as nurse eggs	Young hatch as pelagic veligers, all eggs develop	Same as <i>Buccinanops</i> or ovoviviparous
Egg capsule	Attached to the callous region of the female shell by means of a short pedicle	Always attached to the substrate	Some with filaments retained within the fold of the female's foot or buried below sand surface
Radula	Central tooth with cusps increasing in size towards the center	Central tooth with cusps of the same size, lateral teeth always bicuspidate	Central tooth with cusps of the same size or subequal

decrease in size towards the sides, with one or two central prominent cusps (Figures 4–6). *Bullia* shows rachidian cusps of the same or sub-equal size. *Dorsanum*, too, has similar rachidian teeth, although the cusps are smaller than in the other genera and they are all the same size.

The lateral teeth in *Bullia* show a great variety in number and morphology. Usually they have one or two intermediate cusps. *Buccinanops* always presents more than one intermediate cusp, up to three in the observed specimens. *Dorsanum* always has a bicuspidate lateral tooth.

Buccinanops and *Bullia* bear a carina posterior to the fasciole and a pronounced terminal columellar fold (CERNOHORSKY, 1984; ALLMON, 1990). *Dorsanum*, in contrast, has two oblique spiral carinae bounding a reflexed siphonal channel around the anterior end of the fasciole. These features definitely set *Dorsanum* apart from the other two genera. The shell apices of *Bullia* and *Dorsanum* are more acute and slender than those of *Buccinanops* (according to ALLMON, 1990:plates 5, 6).

Representatives of *Buccinanops* from studied localities are blind, have a well developed foot with one metapodial tentacle, and have large cephalic tentacles. *Bullia* is blind also, has two metapodial tentacles, and has long and slender cephalic tentacles (ALLMON, 1990). Once again, *Dorsanum* differs significantly from the other two genera: it has true eyes, no metapodial tentacles, and short cephalic tentacles (ADAM & KNUDSEN, 1985).

Opercula in *Buccinanops cochlidium* (Table 3), as in other species of the genus, are generally large with smooth margins. They vary little within the genus but differ greatly from those of the other genera. In *Bullia* the operculum is always small, but may be serrated or smooth margined. In *Dorsanum* the operculum is small and smooth margined.

Larval development in *Bullia* and *Buccinanops* shows several similarities, such as nurse eggs, non-planktonic larvae, and young that hatch as crawling veligers. However, the egg capsules are very different. The egg capsules in most species of *Bullia* are carried on the ventral surface of the maternal foot (ALLMON, 1990); the egg capsules are oval, thin, and transparent with two threads at either end. In contrast to the situation in *Bullia* and *Buccinanops*, *Dorsanum* has egg capsules attached to the substrate, pedagic veligers, and no nurse eggs.

ALLMON (1990) considered *Buccinanops* to be a sub-genus of *Bullia* on the basis of three factors: (1) The ranges of their conchological variations overlap; (2) They have non-planktonic larval development and are blind; and (3) *Bullia*, from South Africa and India, was judged to be the direct descendant of *Buccinanops* from South America. The first two factors are correct, although when compared to all the distinguishing features discussed in this paper there is supporting evidence to consider these genera as being distinct. Furthermore, the geographic distributions of *Bullia* and *Buccinanops* suggest two isolated lines of evolution. The idea of South African and Indian *Bullia* deriving from a South American ancestral stock of *Buccinanops* is prob-

ably correct, but that fact is an insufficient reason to subordinate *Buccinanops* to *Bullia*.

According to many characters, having to do with the radula, shell, developmental mode, egg capsule, operculum, and distribution, all the species of *Buccinanops* form an homogeneous group that differs substantially from the species of *Bullia*. Considering all of these, I suggest that *Buccinanops* be accorded full generic status.

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Formation of Organic Sheets in the Inner Shell Layer of *Geloina* (Bivalvia: Corbiculidae): An Adaptive Response to Shell Dissolution

by

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Abstract. Two corbiculids, *Geloina erosa* (Solander) and *G. expansa* (Mousson), from the mangrove swamps of Iriomote Island, southern Japan, occasionally secrete 1–2 μm thick, periostracum-like organic sheets in the inner shell layer. In both species, the organic sheets occur only in specimens which have suffered extensive shell dissolution. Dissolution and organic sheets are especially common in the umbonal region. Numerous microtubes penetrate the inner shell surface in the umbonal region. These microtubes do not extend to the outer shell surface. Each microtube contains soft tissue which seems to perform a sensory function. Such organic sheets are not observed in the shells of other corbiculids living in normal brackish to freshwater environments. The organic sheets in the inner shell layer appear to protect the shell from dissolution. The formation of internal organic sheets in *Geloina* thus can be interpreted as an adaptive response to the acidic mangrove environments, where shell dissolution occurs easily.

INTRODUCTION

Recent corbiculids are euryhaline species occurring in the estuarine and lake environments of brackish to freshwater settings. Most corbiculids develop a thick periostracum to protect the shell from dissolution by acidic water in their habitats. Shell dissolution occurs easily when the periostracum has worn away from the shell surface. In fact full-grown specimens of most corbiculids have suffered shell dissolution in their umbonal region. Shell dissolution of bivalves inhabiting acidic environments have been studied by several workers (GRIER, 1920; TEVESZ & CARTER, 1980; KAT, 1982, 1983; HINCH & GREEN, 1988). Some bivalve species suffering extensive shell dissolution have organic sheets in their shells. Several workers suggested that these organic sheets appear to protect the shell from dissolution (TAYLOR *et al.*, 1969; LEWY & SAMTLEBEN, 1979; TEVESZ & CARTER, 1980; KAT, 1982, 1983, 1985).

Geloina is one of the characteristic corbiculids living in mangrove swamps of tropical to subtropical regions. Species of this genus live in waters having low pH, high temperature, and wide fluctuations in salinity (MORTON, 1975, 1976). They can resist exposure for relatively long periods of time (more than two weeks; MORTON, 1976). Because of the acid soil of mangrove swamps, shell dissolution of *Geloina* occurs more extensively than in cor-

biculids living in other brackish to freshwater environments. *Geloina* has several peculiar shell features, such as a heavy and thick shell, a thick periostracum, and inner periostracum-like organic sheets. These features are interpreted as adaptations to prevent shell dissolution. In this paper, I describe the microscopic features of the inner shell layer of *Geloina* and the degrees of shell dissolution in relation to the bivalve's habitats. I also propose a mechanism for the formation of the internal organic sheets as a response to shell dissolution.

Habitats of *Geloina* and Description of Collection Site

Worldwide, the two major mangrove systems are in the Caribbean and the Indo-Pacific regions. The corbiculid clam *Geloina* occurs in mangrove-dominant brackish-water environments in the Indo-Pacific region, ranging from New Zealand to the Okinawa Islands (Japan) (MORTON, 1983). PRASHAD (1932) classified the Indo-Pacific *Geloina* into three species: *G. erosa* (Solander), *G. bengalensis* (Lamarck), and *G. expansa* (Mousson). Later, MORTON (1983), who reexamined *Geloina* species throughout the Indo-Pacific region, supported PRASHAD's (1932) view.

This paper deals with two species of *Geloina*, *G. erosa* and *G. expansa*, living in mangrove swamps of Iriomote

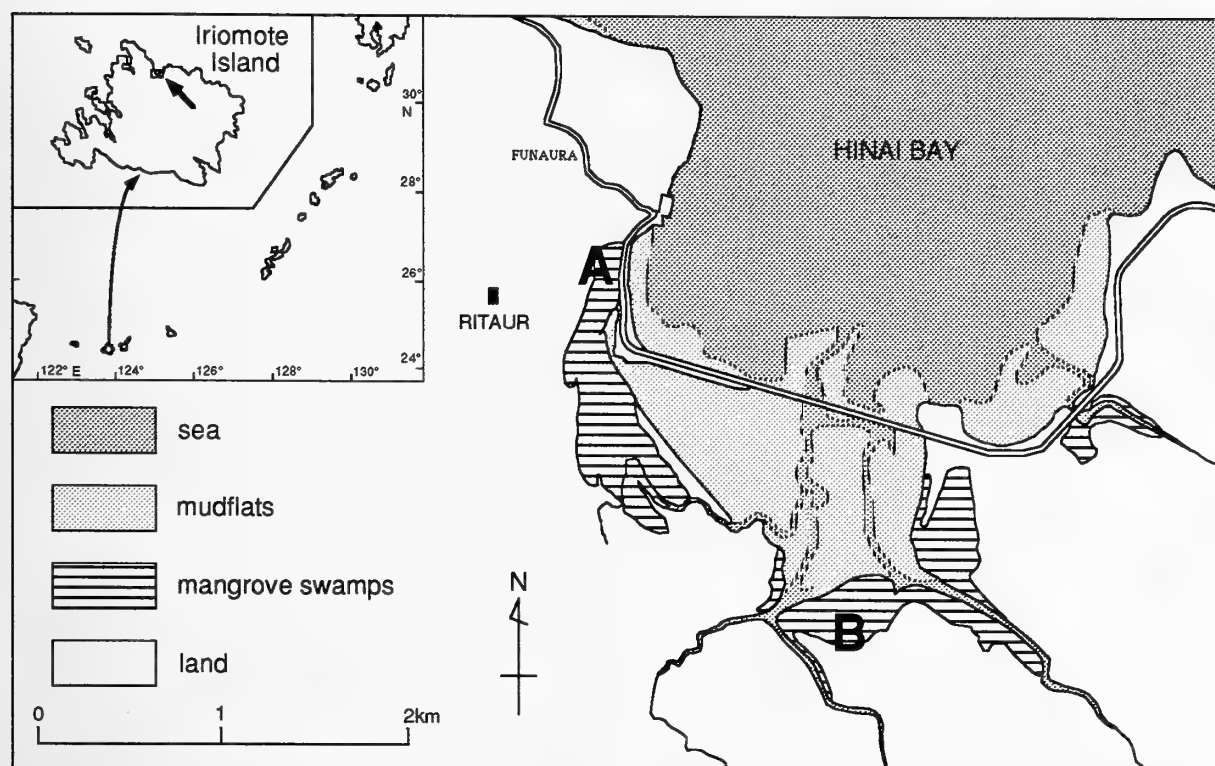


Figure 1

Map showing collecting localities for *Geloina erosa* and *G. expansa*. RITAUR; Research Institute of Tropical Agriculture, University of the Ryukyus. Site A: locality of the specimens without shell dissolution. Site B: locality of the specimens with extensive shell dissolution.

Island, southern Japan. They occur in two different habitats, represented by sites A and B (Figure 1). At site A, during the low spring tides on 24 July 1992, the salinity was 23.2‰. After a heavy rainfall (28 July 1992), the salinity was considerably decreased (to 4.9‰). The pH values of surface and interstitial waters were measured in the two sites at the low spring tides on 29 July 1992 (Table 1). The pH values of surface and interstitial waters at site A were 7.23–7.79 and 6.99–7.24, respectively. The sediment is composed mainly of sand, gravel, and fragments of marine mollusks and corals, but contains no humus. The water is clear. Adjacent lithology is the Pleistocene Ryukyu limestone. No living specimens found at this site

show evidence of shell dissolution in the umbonal region (Figure 2C).

Compared to site A, site B has consistently high salinity and low pH. At the low spring tides on 24 July 1992, the salinity at this site was 27.7‰. Even after a heavy rainfall (28 July 1992), the salinity was 24.8‰. The pH values of surface and interstitial waters were 6.99–7.13 and 5.06–6.54, respectively. At this site, small creeks contain small stagnant pools colored by organic matter. The sediment is composed of muddy, fine sand mixed with humus; it lacks fragments of marine mollusks and corals. Occasionally, small creeks and pools dry out in the landward edge when rainfall is low, suggesting that the landward edge in this

Table 1

Physico-chemical settings of the habitat of *Geloina* on Iriomote Island, southern Japan (site A, site B). The pH values of surface and interstitial waters were measured at the low spring tides on 29 July 1992.

	pH of surface water	pH of interstitial water	Sediment type	Adjacent lithology
Site A	7.23–7.79	6.99–7.24	sand, gravel, fragments of marine mollusks, and corals without humus	limestone (Ryukyu Limestone)
Site B	6.99–7.13	5.06–6.54	muddy fine sand with humus	sandstone and shale (Yae-yama Group)

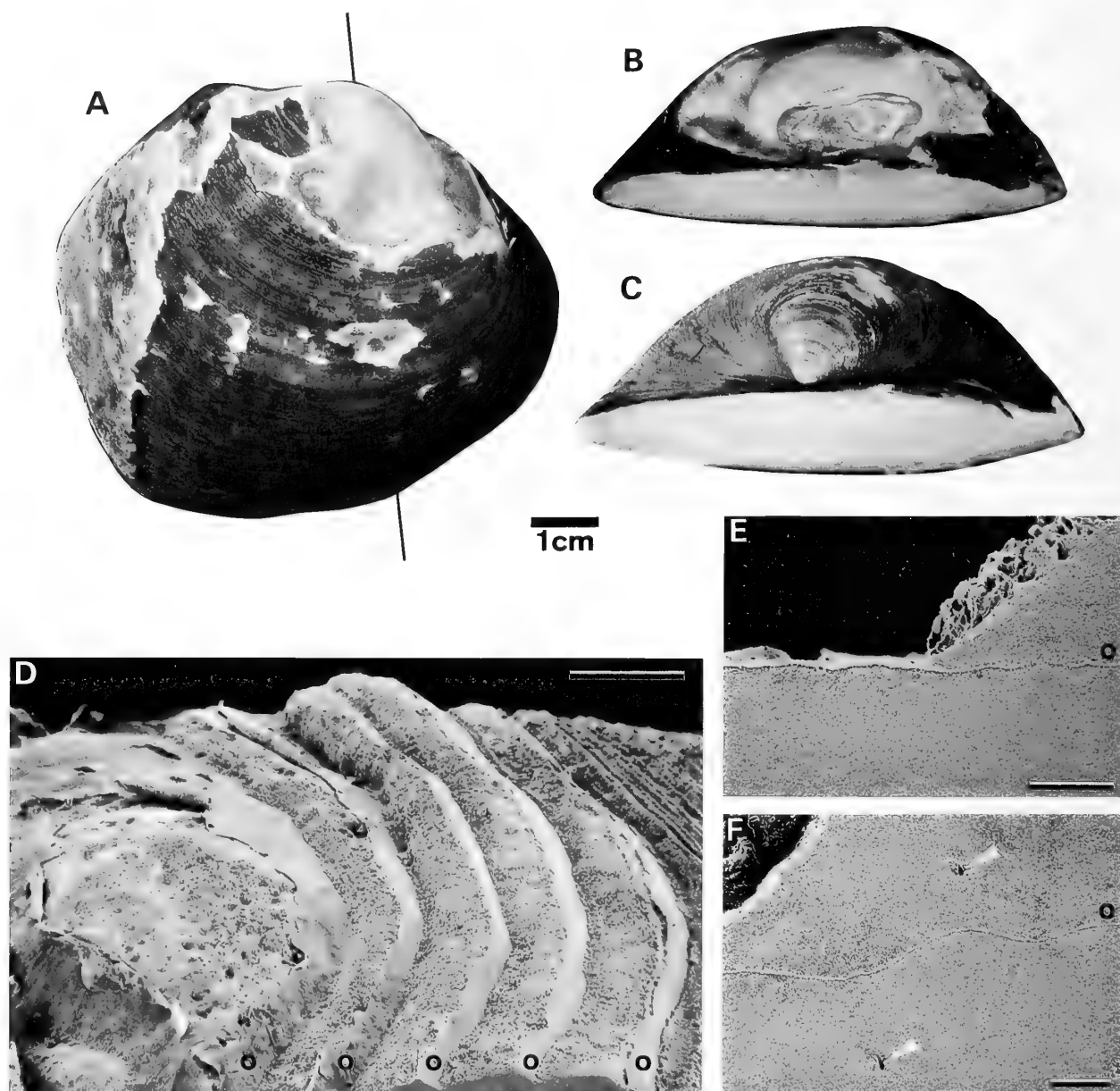


Figure 2

Geloina erosa. A and B. Specimen (UMUT RM 19106) from site B, showing extensive dissolution on the outer shell surface. Organic sheets are exposed in the umbonal region. C. Specimen (UMUT, RM 19107) without extensive shell dissolution from site A. D. Organic sheets in the umbonal region. Same specimen as in A and B. Scale bar: 1 mm. E and F. Organic sheets and microtubes (arrow) on etching surface. Same specimen as in D. Scale bar: 50 μ m. o, organic sheet.

site is rarely covered by seawater. Adjacent lithology is sandstone and shale of the Miocene Yaeyama Group. All living specimens collected from this site have suffered marked shell dissolution in the umbonal region. Specimens occurring in the landward edge, where the duration of desiccation is longer, have suffered deep shell dissolution (Figure 2A, B).

The differences in pH of the water between the two sites are consistent with the degrees of shell dissolution. Acidification of the waters in the mangrove swamps is due to acid sulfate soils and humic acid from humus. It appears to be affected by the duration of dry out and the content of humus. Therefore, long periods of desiccation and high humus content are related to low pH and shell dissolution

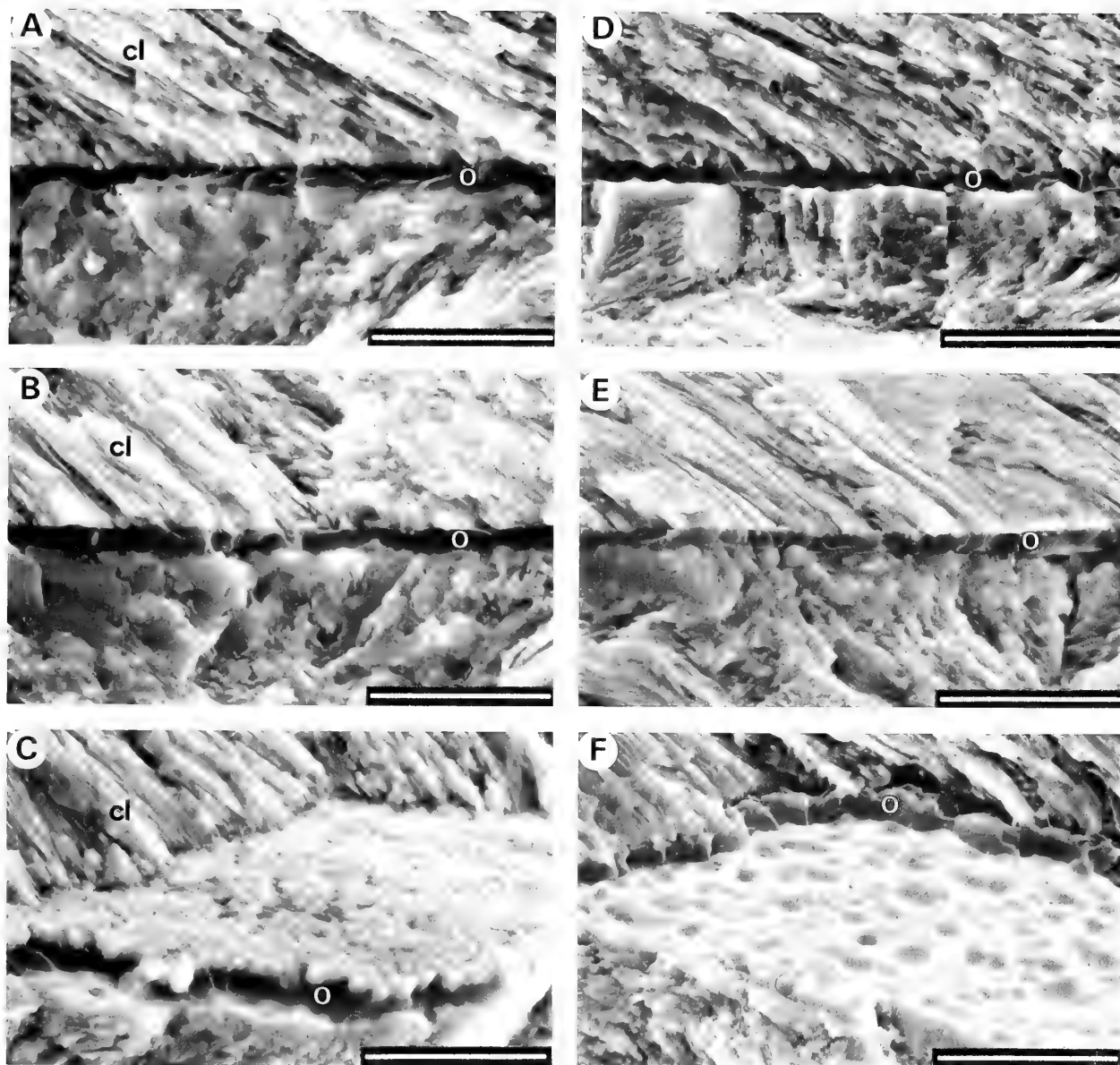


Figure 3

Scanning electron micrographs showing organic sheets in the inner shell layer of *Geloina erosa* (A–C)—same specimen as in Figure 2A—and *Geloina expansa* (D–F)—specimen (UMUT RM 19108) from site B. A and B, D and E. Fractured sections of organic sheets. C. Outer surface of organic sheet. F. Inner surface of organic sheet (mold). Depositional surface is toward the lower. cl, crossed-lamellar layer; o, organic sheet. Scale bar: 10 μ m.

in *Geloina* at site B. On the contrary, fragments of marine mollusks, corals, and limestone present in the sediment appear to buffer the acidic condition of water, which seems to be undersaturated with calcium carbonate at site A.

MATERIALS AND METHODS

Living specimens of *Geloina erosa* and *G. expansa* were collected from two locations in the estuaries of the Hinai River, northern Iriomote Island (Figure 1A, B). After

removing the soft tissue, shells of selected specimens were cut along the umbo-ventral margin, polished, and etched with 5% HCl. Small pieces of the etched shell were coated with platinum, and the internal shell structure was examined by scanning electron microscopy (SEM). SEM observations were also made on fractured shell pieces that were neither polished nor etched. Acetate peels were prepared for etched shell cross sections and studied by optical microscopy. All specimens examined are deposited in the University Museum, University of Tokyo (UMUT).

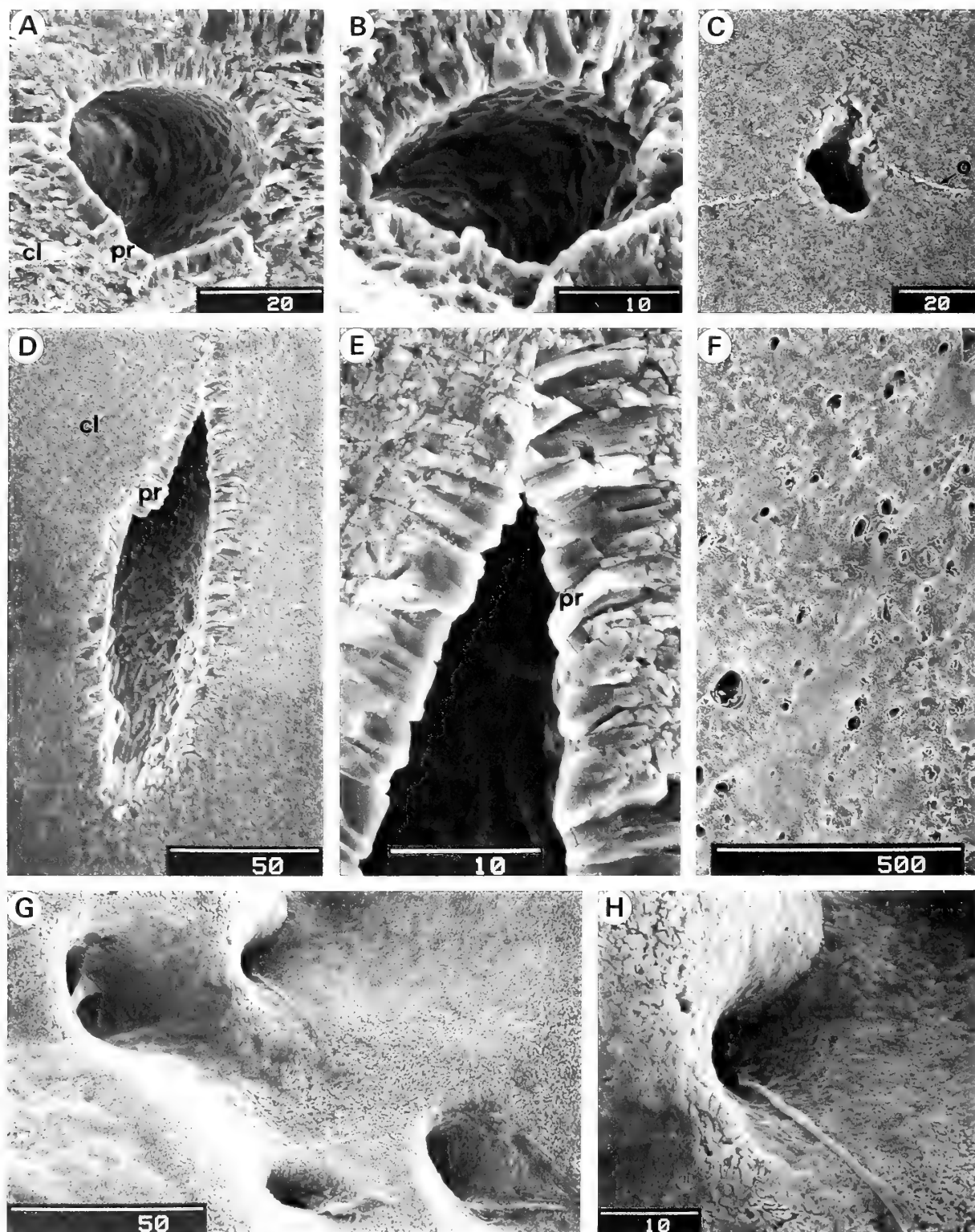


Figure 4

Scanning electron micrographs showing microtubes in the inner shell layer of *Geloina expansa* (A, B) and *G. erosa* (C-H). A and B. Fractured sections of microtubes. Same specimen as in Figure 3D-F. C. Organic sheet, which is curved into a microtube. Same specimen as in Figure 2D-F. D. Microtube located near the inner shell surface. UMUT RM 19109. E. Enlarged view of prismatic wall of the microtube in Figure 4D. F. Openings of microtubes

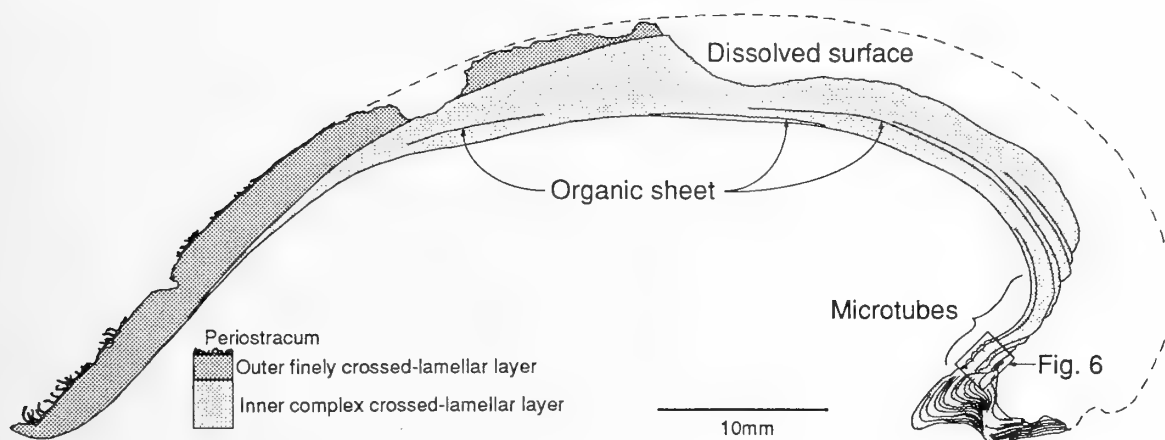


Figure 5

Schematic cross section of the right valve of *Geloina erosa* cut along the line in Figure 2A, showing the position of organic sheets and microtubes.

OBSERVATIONS

The shell of the two *Geloina* species examined consists of an outer layer with a finely crossed-lamellar structure and an inner layer with a complex crossed-lamellar structure, with either an indistinct or thin prismatic pallial myostracum, as in other corbiculid shells (TAYLOR *et al.*, 1973).

In the specimens with marked shell dissolution in the umbonal region, several periostracum-like organic sheets occur in the inner shell layer. The eroded surface of the umbonal region exposes the organic sheets (Figure 2B, D). Therefore, shell dissolution appears to stop temporarily at these organic sheets (Figure 2E).

The organic sheets are 1–2 μm in thickness and occur at irregular intervals ranging from 150 to 500 μm through the shell. The organic material shows a homogeneous structure in the fractured section. In having a homogeneous structure, the organic sheets are very similar to the periostracum (Figure 3), although the periostracum has a sub-layer of vacuoles in the middle part (S. Isaji, unpublished data). These organic sheets are much thicker than the intercrystalline conchiolin layers, which are not observable using SEM on etched cross sections (Figure 2E, F). The outer surface of the organic sheets is flat with a more or less fine granular microstructure (Figure 3C). The inner surface is, in contrast, irregular in shape, with numerous hemispherical granules, about 0.5–2 μm in diameter and 0.2–0.5 μm in height (Figure 3F). The shell structure below the organic sheet has a homogeneous or prismatic structure (5–10 μm thick) (Figure 3A, B, D, E).

When organic sheets are present in the inner shell layer, they always occur in the umbonal region, where extensive

shell dissolution occurs. In highly eroded specimens, the hinge plate shows numerous organic sheets (Figure 5). For example, one such specimen was observed to have 10 organic sheets in the umbonal region and 18 organic sheets in the hinge plate. These sheets decrease in thickness laterally and thin out toward the ventral margins of the shell. In several specimens showing extensive dissolution on the exterior shell surface away from the umbonal region and

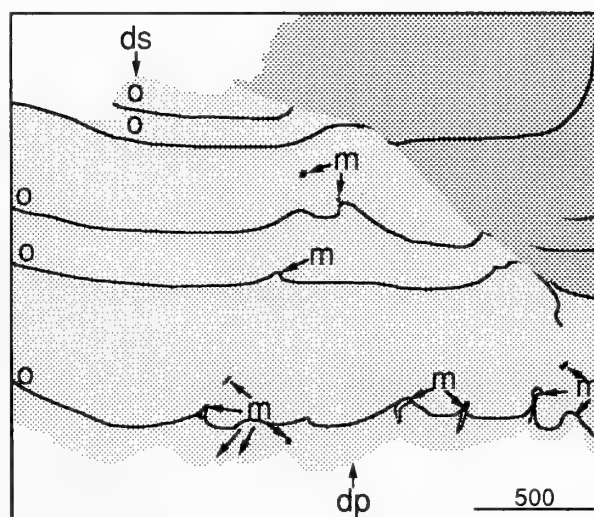


Figure 6

Enlarged view of the inset area in Figure 5. m, microtube; o, organic sheet; ds, dissolved surface; dp, depositional surface. Unit of scale in microns.

← at the depositional surface of the umbonal region. Same specimen as in Figure 4D, E. G. Fibrous substance occurring from the openings of microtubes. UMUT RM 19110. H. Enlarged view of fibrous substance in Figure 4G. Depositional surface is toward the bottom of the figure in Figure 4A–E. The venter is toward the right in Figure 4G. H. cl, crossed-lamellar layer; o, organic sheet; pr, prismatic layer. Unit of scale in microns.

manifest as a deeply dissolved pit, similar organic sheets were observed as irregular patches in the inner shell layer just beneath the deeply dissolved pit (Figure 5). Complete dissolution exposing the outer mantle epithelium was not observed in any specimen. Such organic sheets were not observed in most examined specimens not showing dissolution in the umbonal region.

Besides the organic sheets, numerous microtubes occur locally within the inner shell layer in the umbonal region (Figures 4–6). These microtubes are 10–30 μm in diameter and circular to elliptical in cross section (Figure 4A–D). The inner surface of the microtubes is covered by a thin prismatic wall (about 5–15 μm thick) which is clearly distinguished from the crossed-lamellar structure of the inner shell layer (Figure 4E). These microtubes open into depressions on the inner shell surface around the umbonal cavity (Figure 4F, G). They occur abundantly near the inner shell surface of the umbonal cavity in large specimens but are rare in small specimens. In addition, in one large specimen, these microtubes occur abundantly on the inner side of the inner shell layer but gradually decrease in number toward the outer and ventral sides. The microtubes occur in all specimens regardless of whether or not shell dissolution has occurred. A fibrous substance occasionally occurs within these tubes, which may be the remains of some soft tissue (Figure 4G, H). Numerous micro borings (1 μm in diameter) also occur within both the outer and inner shell layers of the etched area of living specimens. Such micro borings lack thin prismatic walls on their inner surface. These borings appear to be made by endolithic microorganisms (*e.g.*, bacteria, fungi and algae [LILJE-DAHL, 1986]) and are clearly distinguished from microtubes.

No periostracum-like organic sheets have been observed in large specimens of brackish to freshwater corbiculids such as *Corbicula leana* Prime, *C. sandai* Reinhardt, *C. japonica* Prime, all of which have extensive dissolution in their umbonal region (S. Isaji, unpublished data).

DISCUSSION

Judging from their mode of distribution within the shell, periostracum-like organic sheets in the inner shell layer of *Geloina* appear to play a role in retarding the rate of shell dissolution. Most mollusks can repair their shell. BEEDHAM (1965) stated that *Anodonta* secretes organic sheets on the outer mantle surface when the shell is damaged. WATABE (1983) also documented that internal organic sheets are observable in the repaired shells of several bivalve genera. In the case of *Geloina*, no specimens were observed whose umbonal region was completely eroded. Therefore, the organic sheets in the inner shell layer of *Geloina* were not secreted as damage-repair sheets. The restricted distribution of the organic sheets in the inner shell layer suggests that they were deposited in response to deep dissolution on the shell surface. Therefore, they

appear to have secreted from the inside of the shell by the mantle epithelium before the dissolution reached the internal shell surface. According to KAT (1985), *Geloina suborbiculata* (Pilsbry) has organic sheets (4–6 μm in thickness) in the inner shell layer and no more than two organic sheets were observed to occur in the shell of examined specimens. The differences in information about the thickness and number of organic sheets presented by KAT (1985) and in this study may be due to both species differences and degrees of shell dissolution of the examined specimens.

Similar organic sheets have been found in the bivalve shells of several different taxa. KAT (1985) reported that organic sheets occur within the shell of some marine and brackish-water bivalve species distributed among three superfamilies (Solenacea, Corbiculacea, and Myacea) and are ubiquitous among freshwater Unionacea (see also TOLSTIKOVA, 1974). Such organic sheets may have an important role in retarding the rate of shell dissolution under the low pH conditions of their habitats (TAYLOR *et al.*, 1969; TEVESZ & CARTER, 1980; KAT, 1982, 1983, 1985). LEWY & SAMTLEBEN (1979) also reported the presence of internal organic sheets in corbulid shells, which they interpreted as resisting both predation by boring gastropods and shell dissolution. KAT (1985) also reported the similarities of microstructural features of organic sheets existing in four different superfamilies. He stated that "these convergences may have arisen through a similarity of responses to similar selection pressures and to constraints on the number of ways such organic sheets can be constructed."

In the case of the Unionacea, extensively eroded shells have more numerous organic sheets than the shells without appreciable umbonal dissolution (TEVESZ & CARTER, 1980; KAT, 1983). Extensive shell dissolution can take place without lethal effects in the Unionacea. TEVESZ & CARTER (1980) have suggested that unionids can deposit patches of adventitious organic sheets near their umbonal region as a safeguard against possible deep umbonal dissolution. According to these authors, these prophylactic organic sheets can be distinguished from damage-repair sheets by their lack of an underlying prismatic layer. It is uncertain, however, what kind of factor causes the formation of these prophylactic organic sheets of unionid shells (KAT, 1983).

In all *Geloina* specimens that have suffered extensive shell dissolution in the umbonal region, microtubes occur locally within the inner shell layer in association with internal organic sheets. This correlation suggests that the microtubes may somehow be related to the formation of internal organic sheets in the inner shell layer. For instance, the microtubes may have housed soft tissue, and the tissue may have a sensory function related to the detection of shell dissolution. This hypothesis could be tested in part by histochemical examination of the soft tissue found in the microtubes.

Tiny canals (3–9 μm in diameter) similar to those observed in *Geloina* shells are known to occur in the small

freshwater corbiculids of the family Pisidiidae. These canals in the shells of the Pisidiidae are called punctae (ROSSO, 1954; ROBERTSON & CONEY, 1979). These punctae tunnel through both inner and outer shell layers but not through the periostracum layer. They are distributed broadly on the shell disc even in prodissoconch larval shells. All of the punctae housed tube-shaped projections of the outer mantle tissue (ROSSO, 1954; ROBERTSON & CONEY, 1979). ROBERTSON & CONEY (1979) speculated that the punctae of *Musculium securis* (Prime) have a special function for respiration and/or monitoring the moisture content. The function of these punctae is unknown. In their mode of distribution within the shells, the punctae of Pisidiidae differ from those of *Geloina*.

HINCH & GREEN (1988) suggested that dissolution of the unionid shell is not related to differences in ambient water chemistry. They argued that shell dissolution in unionids is primarily a physical process probably related to water turbulence. It is certain that shell dissolution is initiated by abrasion of the periostracum of the umbonal region. However, once the periostracum has worn away, shell dissolution seems to be accelerated by low pH of the ambient water. In mangrove swamps, shell dissolution in *Geloina* does not appear to be affected by a difference in the grain size of the sediment of the habitats. Therefore, acidification of water in the mangrove swamps is assumed to be a major source of shell dissolution in *Geloina*. In addition, low water turbulence within the mangrove swamps promotes the chemical process of shell dissolution. On the other hand, acidic water is common in normal brackish to freshwater environments. Most large-sized specimens of the Corbiculidae inhabiting such environments possess an eroded umbo. However, no distinct internal organic sheets have been observed in other corbiculid shells inhabiting brackish to freshwater environments, although shell dissolution in the umbonal region is lethal (KAT, 1982). In contrast, *Geloina* species can secrete internal organic sheets that prevent extensive shell dissolution when the inner shell layer is exposed to the ambient water through exfoliation of the periostracum. These organic sheets permit survival of *Geloina* in mangrove swamps, where chemical shell dissolution occurs more easily than in normal brackish to freshwater environments.

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A New Species of *Cypraea* from Samoa in the *C. cribraria* complex

by

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Abstract. *Cypraea taitae*, the eighth member of the *C. cribraria* complex of cowries, is described as a new species on the basis of conchological and external anatomical features which differ from those in *C. astaryi* Schilder, 1971, a close conchological relative, and from all others in the *C. cribraria* species complex. *Cypraea fallax* Smith, 1880, and *C. bernardi* Richard, 1974, are not considered members of the *C. cribraria* species complex.

Cypraea taitae Burgess, sp. nov.

(Figures 1-4, 8, 10)

Description: Shell: Cypraeiform, elongate-ovoid, moderately small, 10-17 mm, with produced extremities. Labial callus prominent; slightly umbilicated. Anterior extremity prominent and pointing upward in two of the five paratypes. Columellar teeth fine, sharply cut, confined to aperture. Labial teeth slightly coarser, produced to cross about one-third of the base. Aperture narrow, curved toward the columellar lip. Fossula vertical, prominently ribbed with six denticles but without a sulcus. Dorsum gold colored with discrete white spots; mantle line definite and discrete. Spire pure white but dorsal pigment may encroach. Discrete brown to black spots (0.3×0.7 mm) confined to the top of the labial callus and not appearing to ascend onto dorsum; spots not always visible on lateral margin of labial base. Columella with similar spots confined almost always to lateral margins of white base.

Animal characters: Mantle brilliant dark carmine, thin, not obscuring dorsal pattern. Papillae fingerlike, blunt, arising from circular area of discrete black dots. Other papillae prominent, widely spaced, resembling three or four beads on a string, decreasing in size from their bases. Some papillae white, bearing several tufts arising from terminal bead, forming two vertical rows equally spaced along full length of mantle. Siphon carmine, finely fringed with short processes shaped exactly like interstices between them. Tentacles darker carmine, clubbed, with still darker tips. Foot of same color as mantle, studded, as is mantle, with discrete black spots; crawling surface pale orange.

Habitat: Three live specimens were collected by the author in 1965, near Lepua Village, Pago Pago, Tutuila, Amer-

ican Samoa, on the north side of the harbor on the reef flat; the cowries were under large coral blocks at a depth of 1-3 m at low tide near the drop-off into deep water. Additional specimens were collected from the same area by Bob Purtymun (personal communication, 1977) who also found subfossil shells in Pago Pago Harbor dredgings at Aua. In Western Samoa, Terry Kurth (personal communication, 1975) collected three pairs, each of one large and one small specimen, at 7.6 m in a current-swept gap in the reef under small coral slabs.

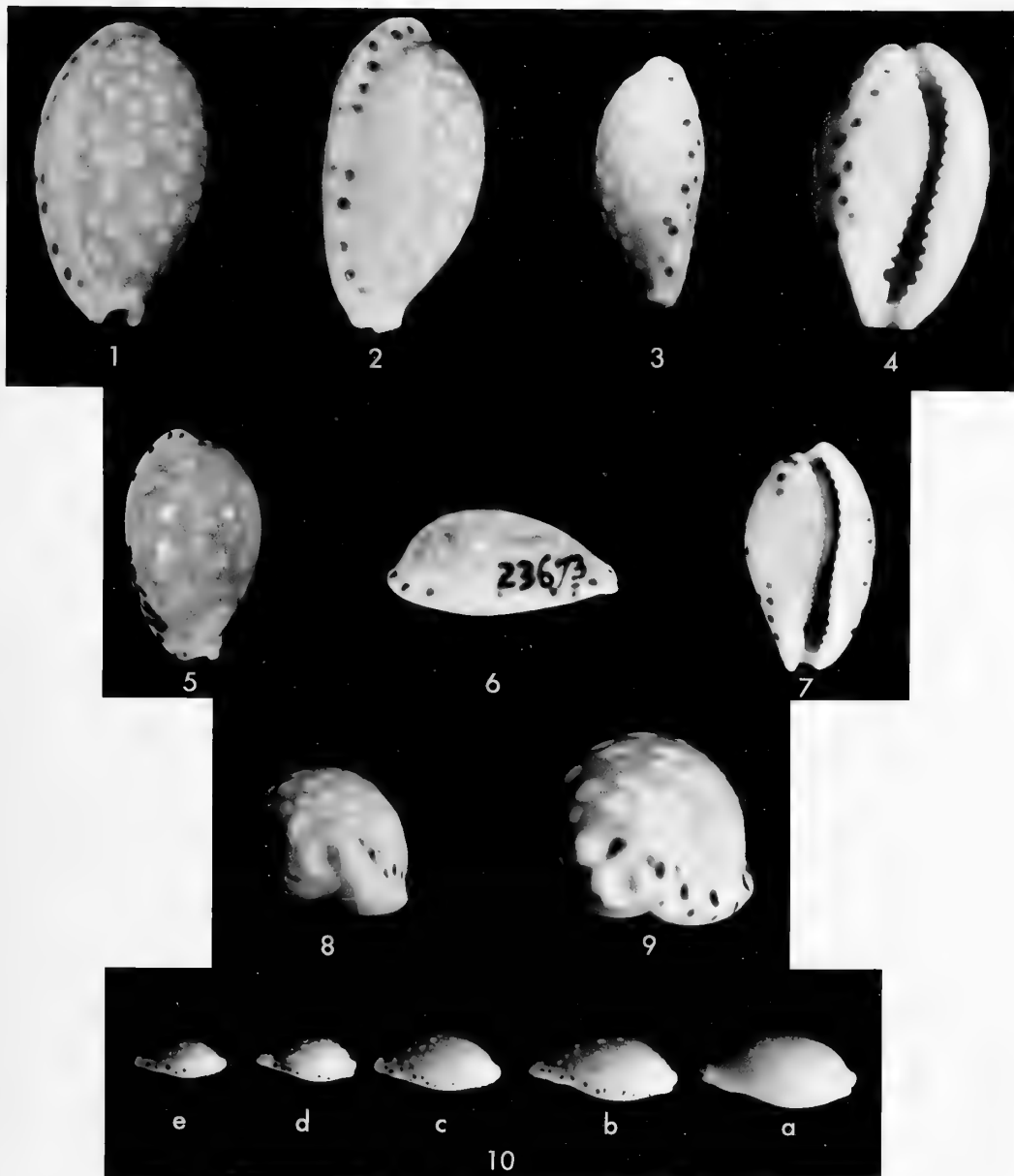
Measurements: See Table 1.

Type locality: The reef near the village of Lepua directly across Pago Pago Harbor from the city, Tutuila, American Samoa, 140°W, 19°6'S.

Range: American Samoa (C. M. Burgess & R. Purtymun, personal communication, 1977); Western Samoa (T. Kurth, personal communication, 1983); Fiji (CERNOHORSKY, 1965, *non C. gaskoini*); New Hebrides (now Vanuatu) (SCHILDER & CERNOHORSKY, 1967; DEBANT 1969, *non C. fischeri* Vayssi re, 1910).

Type depository: The holotype, length 16.2 mm, width 9.4 mm, is deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii, BPBM 9966. Paratypes "a" and "b" (Figure 1) are in the Purtymun collection, 1200 Brickyard Way, No. 407, Point Richmond, California 94801; paratypes "c" and "e" (Figure 1) are in the Burgess collection, 2502 Manoa Road, Honolulu, Hawaii 96822; paratype "d" is in the McKinsey collection, 95-016 Kipapa Drive, Miliolani, Hawaii 96789.

Etymology: This species is named for my wife, Grace Tait Burgess, whose love and willingness to continue to



Explanation of Figures 1 to 10

Figures 1-4. Dorsal, right and left lateral, and ventral views of the holotype of *Cypraea taitae*. BPBM 9966. Produced extremities are clearly illustrated. 16.2 × 9.4 mm. Photo by O. Schoenberg-Dole. ×1.25

Figures 5-7. Dorsal, right lateral, and ventral views of the holotype of *C. astaryi*. 16.6 mm. Photos by E. Alison Kay. ×1.25

Figures 8, 9. Spire views of the holotype of *C. taitae* (Figure 8), and a homeotype of *C. astaryi* from the Tuamotu Archipelago (Figure 9). Pigmented spire clearly illustrated. Photos by O. Schoenberg-Dole. ×1.25

Figure 10. Left lateral views of the five paratypes of *C. taitae*. a. length 17.0, width 9.8 mm; b. length 15.8, width 8.8 mm; c. length 13.6, width 7.7 mm; d. length 10.7, width 5.7 mm; e. length 9.8, width 5.10 mm. Photos by O. Schoenberg-Dole. ×1.25

Table 1
Cypraea taitae. Measurements and ratios.

Depository	Catalogue number	Locality	Length (mm)	Width (mm)	Height (mm)	L/W ratio	L/H ratio	Labial teeth	Columnar teeth
Bishop Museum	BPBM 9966 (Burgess 756-1) holotype	Lepua, American Samoa	16.2	9.4	7.1	1.72	2.28	16	22
Purtymun	10003 paratype a	Aua, American Samoa	17.0	9.8	7.5	1.73	2.27	18	27
Purtymun	10002 paratype b	Lepua, American Samoa	15.8	8.8	6.9	1.79	2.29	17	23
Burgess	756-2 paratype c	Lepua, American Samoa	13.6	7.7	6	1.77	2.27	15	20
McKinsey	FO16A4 paratype d	Taema Bank, American Samoa	10.7	5.7	5	1.88	2.14	16	19
Burgess	756-3 paratype e	Asau, Western Samoa	9.8	5.1	4.4	1.92	2.23	15	18
Average			13.85	7.75	6.15	1.8	2.25	16.1	21.5

type and retype unfamiliar words and names over almost a lifetime built a debt that I can never repay.

Comparisons: *Cypraea taitae* is the eighth member of the *C. cribraria* group, species of which are characterized by their orange to reddish dorsal pigmentation. Shells of *C. taitae* are easily separated from all others in the complex, and differ from those of *C. cribraria* Linnaeus, 1758, *C. cribellum*, Gaskoin 1849, and *C. catholicorum* Schilder & Schilder, 1938, by the presence of prominent discrete brown to black spots on the columellar and labial margins. Occasional small pigmented blotches or a few tiny light brown flecks may be present on the shells of each of these three species, but cannot be confused with the prominent spotting of *C. taitae*. The shells of *C. gaskoini* Reeve, 1846, differ from those of *C. taitae* in that they are globose; also, the marginal spots are smaller and in fully adult specimens may cover much of the dorsum of the shell. The shells of *C. esontropia* Duclos, 1833, are larger (14–34.7 mm) and more globose than those of *C. taitae*, the dark-banded embryonal structure is visible through the larger dorsal spots, and the teeth are much coarser than those in *C. taitae*. In *C. cumingi* Sowerby, 1832, the teeth are much finer and the terminal margin of the anterior lip is concave and sharper than in *C. taitae*.

Conchologically, shells of *Cypraea taitae* are most like those of *C. astaryi* (Schilder, 1971) (Figures 5–7, 9) but they differ in several respects. The anterior extremity of *C. taitae* is produced to the point where it is actually directed upward and extends from the shell to a prominent degree, and to a greater degree in two of the five paratypes. The shallow umbilicus of *C. taitae* is pure white and is without pigment except for the slight encroachment of the dorsal pattern; the umbilicus of *C. astaryi* is a narrow but deep, pigmented pit. The posterior extremity of *C. taitae*

is prominent but not so prominent as is the anterior extremity; the anterior extremity of *C. astaryi* is barely visible and in most specimens blends smoothly with the curve of the dorsum, a difference clearly seen in lateral views of both cowries. The shells of *C. taitae* are slender; those of *C. astaryi* (in all 17 specimens studied) are plump and loaf-shaped. The dorsal spots of *C. taitae* are rarely (one of six of the type lot) rimmed with a barely visible darker pigment ring which is a prominent character of *C. astaryi*. The teeth of both species are similar in number and appearance. In *C. astaryi* the fossula is grooved and grossly ridged; in *C. taitae* it is shallow and receding. The shells in both species have prominent marginal spotting but in *C. astaryi* it is more profuse and the spots are larger and often more heavily pigmented. Only the edges of the labial basilar spots of *C. taitae* are visible on the extreme lateral margins; the spots in *C. astaryi* are prominent and cover a portion of the base.

The mantle characters in *Cypraea taitae* are also very distinctive; indeed, it is the only member of the *C. cribraria* species complex that has tufted papillae. The mantle is also distinguished from that in *C. astaryi* by the papillar arrangement and by the discrete black spots which stud it and the foot. Neither tufted papillae nor the spots are present on the mantle of *C. astaryi* (see Busson's photograph of the mantle of *C. astaryi* in BURGESS (1985:250).

Discussion and History

From 1965 to 1985, references to *Cypraea astaryi*, *C. gaskoini*, and *C. fischeri* have been utterly confused. In 1986 André Lefait of Papeete, Tahiti, sent me a number of cowries from the Marquesas Islands and the Tuamotu Archipelago that did not fit any of the descriptions of shells in the *C. cribraria* species-complex. Comparison with the

holotype of *C. astaryi*, however, showed that they were conspecific with that species. Similarly, comparison of the type of *C. fischeri* with an array of shells in the *C. cribraria* species-complex showed that it was conspecific with *C. gaskoini*. These determinations left the shells described here as *C. taitae* without a name, a circumstance now rectified.

There are also some previously published figures both of shells and animals of *Cypraea taitae* which were ascribed to other species. These references include those of CERNOHORSKY (1965:3, figs. 1-4) who cites the shells as *C. gaskoini* from Fiji; SCHILDER & CERNOHORSKY (1967: 6, figs. 2, 3) who cites the shells as *C. cumingii* from the New Hebrides; DEBANT (1969:6, fig. 1a, b) who also refers his shells to *C. cumingii* from the New Hebrides; BURGESS (1977: 2, unnumbered text figures); and BURGESS (1985: 250, unnumbered figure) who refers his illustrations and animal description to *C. astaryi*. BURGESS (1985) was not aware that his Samoan *Cypraea* species was specifically different from *C. astaryi* and the illustrations of the dorsal and ventral views of what was then thought to represent that species are those of *C. taitae*; the photograph of the animal is, however, that of *C. astaryi*.

Two additional species have been suggested as members of the *Cypraea cribraria* species-complex: *C. fallax* Smith, 1880 (see LORENZ & BIRAGHI, 1986) (= *Cribraria haddnighiae* Trenberth, 1973) and *C. bernardi* Richard, 1974. Both conchological and mantle characters suggest that they are members of a group of *Cypraea* other than that of the *C. cribraria* species-complex. The shells of *C. fallax* reported from Denmark Beach, near Albany, Western Australia (BURGESS, 1985), superficially resemble those of *C. cribraria*, but the dorsal spotting is not depressed as in the shells of *C. cribraria* and others in the complex (the depression is formed by a lack of deposition of the dorsal pigment). The spots are more variable in size, the teeth on the columella are more produced, the fossula is of a different type (consisting of a very prominent and grossly ridged structure), the mantle obscures the dorsal pattern, and the thick conical papillae on the mantle differ from the slender, sometimes tufted, beaded papillae in the *C. cribraria* species-complex. The shells of *C. bernardi* Richard, 1974, from Hitiaa, Tahiti similarly lack the depressed dorsal spotting in the *C. cribraria* species-complex; the spots are more variable in size, the labial and columellar teeth are much heavier than they are in shells of other species in the complex, and the mantle is yellow-brown with thick fingerlike papillae with blunt white tips.

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C. taitae from Samoa that serve as paratypes (a and b); and to Ray McKinsey for the loan of his paratype (d). I am most grateful for the indispensable guidance given by Dr. E. Alison Kay, Professor of Zoology at the University of Hawaii, not only in the formation of this presentation but also for her shared knowledge of the Cypraeidae over many years. It was Dr. Kay who borrowed the holotypes that were so vital in establishing a new species. And, sincere thanks to Olive Schoenberg-Dole for the sharp photographs shown here as Figures 1-4, 8-10.

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How Does *Strombina* Reproduce? Evidence from Two Venezuelan Species (Prosobranchia: Columbelloidea)

by

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Abstract. The objective of this paper is to describe the spawn and the reproductive strategy of *Strombina francesae* and *S. pumilio*. Spawn of both species consists of grayish-white and dome-shaped egg capsules that are laid as a compact mass on living adult shells of the same species. The egg capsules of *S. francesae*, obtained at the Archipiélago de Los Roques, have a closed oval escape aperture at their top. In each egg capsule, five eggs that measure $571 \pm 35 \mu\text{m}$ ($n = 22$ eggs) in diameter develop into embryos. Even though hatching was not directly observed, the absence of a velum and the presence of well-developed structures in late embryos indicate that hatchlings emerge from the egg capsules as crawling juveniles. The egg capsules of different specimens of *S. pumilio* were obtained at Bahía de Mochima and Isla Caribe. In each egg capsule, 3 to 5 eggs develop into embryos. The egg diameter of one spawn from Isla Caribe was $616 \pm 48 \mu\text{m}$ ($n = 22$ eggs). Juveniles hatching from one spawn found at Las Maritas crawled out from an oval escape aperture located at one side of the case wall. No evidence of nurse eggs was found in egg capsules of either species. The simple domed egg-capsule shape has been reported for other columbellids and also for other families of gastropods. According to the literature we have reviewed, the egg diameters herein reported are the largest in the Columbelloidea.

INTRODUCTION

Only six living species of *Strombina* Mörch, 1852, have been reported for the western Atlantic: the first two recorded were *Strombina pumilio* (Reeve, 1859), from Cumaná, eastern Venezuela, and *Strombina francesae* J. Gibson-Smith, in J. Gibson-Smith & W. Gibson-Smith, 1974, from Cayo Francés, Archipiélago de Los Roques (VINK, 1979; JUNG, 1986, 1989). By contrast, 32 species of *Strombina* and related genera inhabit the eastern Pacific. This remarkable diversity difference has been mainly explained by the massive and wide-spread extinction of mollusks that occurred in the Caribbean province from the middle Pliocene to the Pleistocene (VERMEIJ, 1978; JUNG, 1989). Due to the scarcity of information on the life habits of these genera, biological studies on these Caribbean species would give new insights to paleontology and biogeography research. Only indirect evidence of larval development of *Sincola* and *Bifurcium* (JUNG, 1986, 1989), and a statement on direct development of *S. pumilio* (PENCHASZADEH, 1988), have been previously reported. There is, however, a large number of reports dealing with the spawning and larvae of other columbellids (e.g., PETIT & RISBEC, 1929; THORSON, 1940; FRANC, 1941; BACCI, 1947; KNUDSEN, 1950; NATARAJAN, 1957; MARCUS & MARCUS, 1962; AMIO,

1963; SCHELTEMA & SCHELTEMA, 1963; SCHELTEMA, 1969; RAEIHLE, 1969; D'ASARO, 1970; BANDEL, 1974; FLORES, 1978). The following is the first description of the spawn of *S. francesae* and *S. pumilio*.

MATERIALS AND METHODS

The identification of *Strombina francesae* (Figure 1A) and *S. pumilio* (Figure 1B) follows JUNG (1989). Spawns of *Strombina* spp. were deposited at the Museo de Ciencias Naturales de la Universidad Simón Bolívar (MCNUSB). Scientific names have been cited as in the original reports.

Observations on the egg capsules of *Strombina francesae* were made on those attached to one specimen (MCNUSB-H266), obtained by Donald Shasky in March 1990 at Cayo Dos Mosquises (Figure 2A), southwest of Archipiélago de Los Roques ($11^{\circ}48'26''\text{N}$, $66^{\circ}53'16''\text{W}$). Information about the egg capsules of *S. pumilio* was obtained from one specimen (MCNUSB-H267) captured in September 1985 at Las Maritas (Figure 2B), a sandy beach at Bahía de Mochima ($10^{\circ}24'11''\text{N}$, $64^{\circ}20'00''\text{W}$) and from the egg capsules attached to three specimens captured at Isla Caribe (Figure 2C), a small island located on the northern coast of the Península de Araya ($10^{\circ}42'11''\text{N}$, $63^{\circ}52'57''\text{W}$): one of them was obtained in June 1991

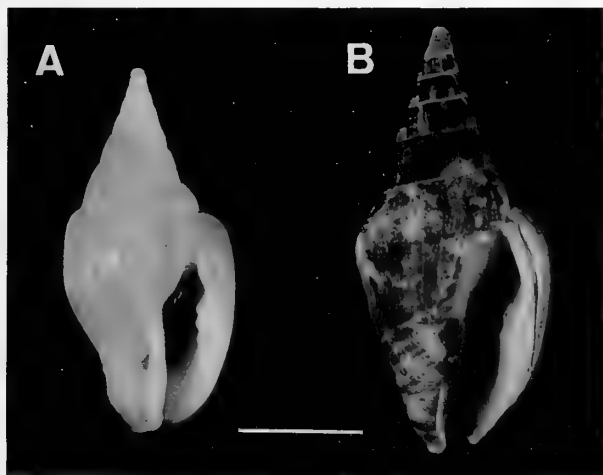


Figure 1

A. *Strombina francesae*, from Dos Mosquises Sur. B. *Strombina pumilio*, from Isla Caribe. Scale bar: 5 mm.

(MCNUSB-H144), another specimen was captured in September 1991 (MCNUSB-H217), and the final one was collected in March 1992 (MCNUSB-H253).

Hatchlings of *Strombina pumilio* were obtained from the egg capsules attached to one specimen that was captured at Las Maritas, brought to the laboratory, and maintained in an aquarium with aerated seawater.

Length, width, height, aperture length, and aperture width were measured in egg capsules from different spec-

imens. The minimum straight distance, perpendicular to the length, measured from the lower border of the escape aperture to the border of the egg capsule base, was used as an indicator of the relative position of the escape aperture. This variable was defined as the *aperture position* and is listed in Table 1. The egg diameter of both species was determined from fixed, uncleaved zygotes. Uncleaved eggs, individuals at the trocophore stage, and early and late embryos were all counted from different egg capsules of single spawns to indirectly ascertain the presence of nurse eggs. Shell length of hatchlings and late embryos was measured from the tip of the shell to the tip of the siphon canal. Shell width was the maximum width, perpendicular to the length. Both measurements were obtained with the shell aperture facing down. The counting of the number of whorls follows JUNG (1986). Measurements were made using a Zeiss Stemi IV stereoscopic microscope.

An electron microscope (Phillips T-SEM 505) was used to photograph adult protoconchs, juvenile shells, and egg capsules. This material was cleaned with filtered seawater and kept in a 70% ethanol solution before being coated with gold. SEM photographs of adult protoconchs and juvenile shells were compared to confirm the identity of hatchlings.

RESULTS

Strombina francesae

The specimen of *Strombina francesae* was found buried about 2 cm deep in coarse sand, in a sandy area covered

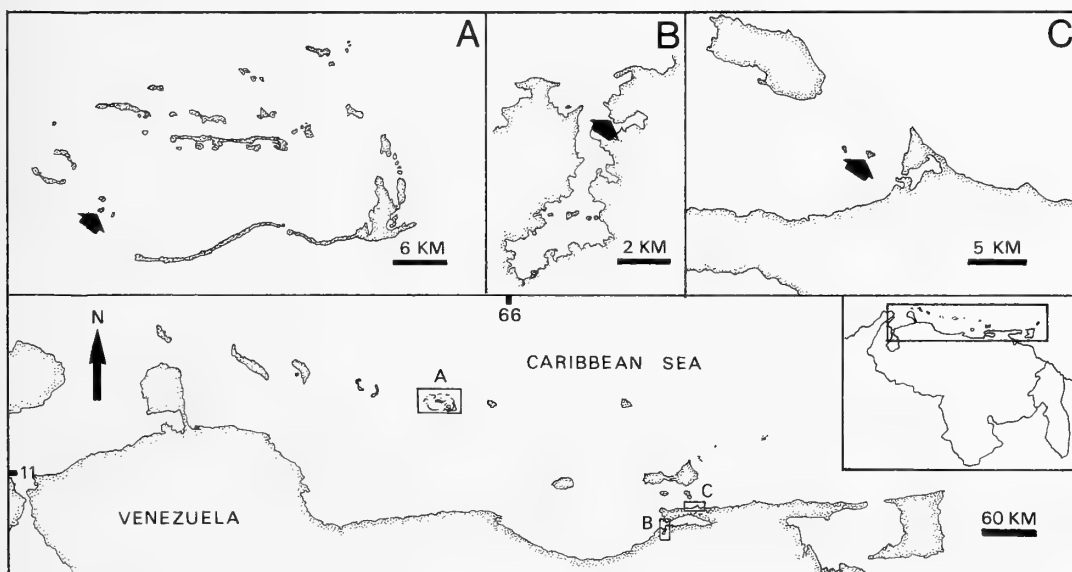


Figure 2

The three sampling areas of *Strombina* spp. on the Venezuelan coast are shown as A, B, and C on the bottom map. These areas are shown enlarged on the top. The black arrows on each map indicate the sampling sites. A. Archipiélago de Los Roques National Park. Arrow: Dos Mosquises area. B. Bahía de Mochima. Arrow: Las Maritas Beach. C. Detail of the northern coast of the Península de Araya. Arrow: Isla Caribe.

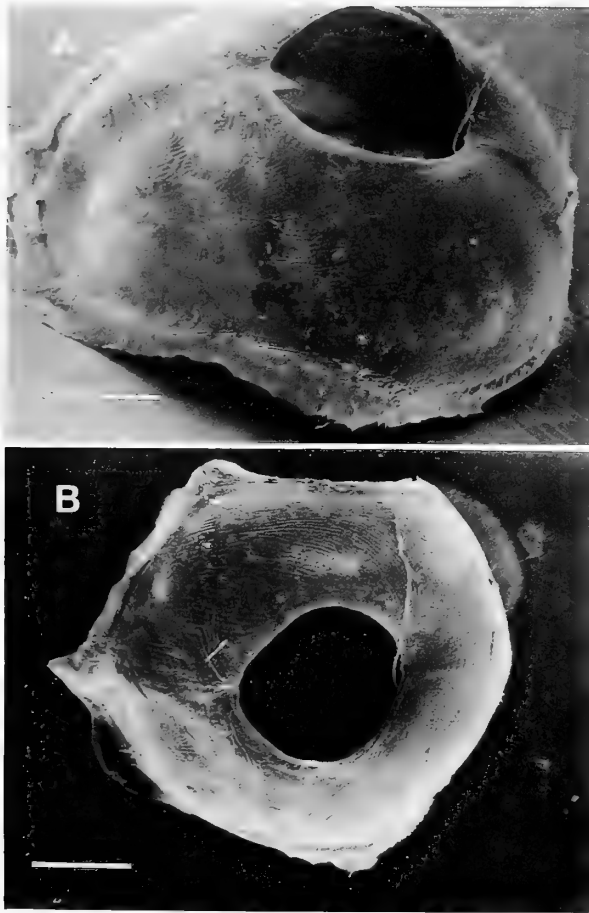


Figure 3

SEM pictures of an egg capsule of *Strombina francesae* from Dos Mosquises. The membrane of the escape aperture has been removed. A. Side view. B. Top view. Scale bar: 0.5 mm.

by algal drift, at 0.8 m depth. It measured 17 mm in total length.

Almost all the egg capsules were arranged in a compact mass covering most of the body whorl and the last three teleoconch whorls. They were grayish-white, translucent, and semispherical (Figure 3A, B; Table 1). Their surface

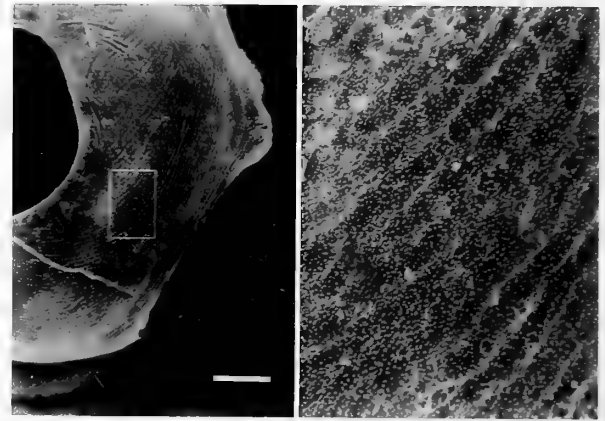


Figure 4

SEM detail of the surface of the egg capsule of *Strombina francesae* from Dos Mosquises. The enclosed area is enlarged on the right side of the figure. Scale bar: 0.25 mm.

had small, faint and sinuous grooves that resembled a "fingerprint" (Figure 4). Their basal wall was usually oval and slightly concave but it was irregularly shaped when the egg capsules were tightly attached to each other or when they were laid over other egg capsules. There was a thin and narrow ringed flange around the base of each egg capsule, the border of which was always irregularly broken. There was a suture on the egg capsule wall running longitudinally from one side of the egg capsule to the other, dividing it into two almost equal halves. Near the center of the egg capsule, the suture borders separated from each other, forming an oval escape aperture, which was covered by a thin, almost smooth and opaque membrane.

Uncleaved zygotes, trocophore stages, and early and late embryos were all found in different egg capsules of the single studied mass, suggesting that it was formed by more than one spawn (Table 2). Eggs measured $571 \pm 35 \mu\text{m}$ ($n = 22$ eggs) in diameter. No evidence of nurse eggs was found. Of the seven fixed egg capsules that contained well-developed individuals, only 24 shells from late embryos were intact, having from 1.25 to 1.5 whorls and measuring 990

Table 1

Dimensions of the egg capsules of *Strombina francesae* and *S. pumilio*. Data obtained from 12 egg capsules of each species are given in millimeters (mm). The MCNUSB catalog number is under the scientific name. The information is presented as mean \pm standard deviation.

Species	Length	Width	Height	Aperture length	Aperture width	Aperture position
<i>Strombina francesae</i>						
H266	2.4 ± 0.3	2.1 ± 0.2	1.3 ± 0.1	1.3 ± 0.3	0.9 ± 0.05	0.5 ± 0.10
<i>Strombina pumilio</i>						
H267	2.4 ± 0.2	2.1 ± 0.1	1.5 ± 0.2	1.3 ± 0.1	1.1 ± 0.1	0.1 ± 0.05
<i>Strombina pumilio</i>						
H217	2.1 ± 0.1	2.0 ± 0.2	1.4 ± 0.3	1.3 ± 0.1	1.0 ± 0.2	0.2 ± 0.14

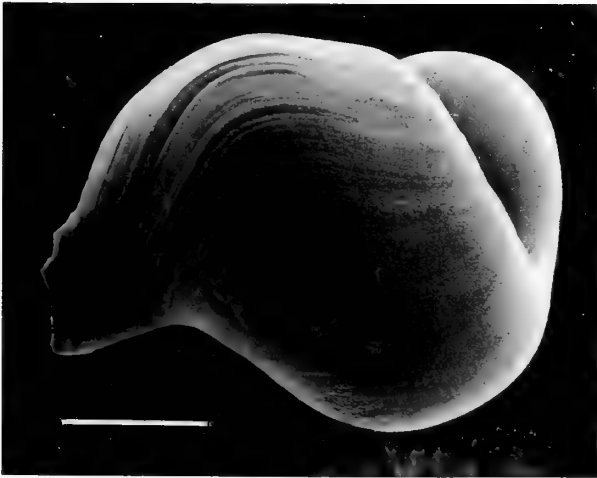


Figure 5

SEM picture of a late embryo shell of *Strombina francesae*. Scale bar: 0.25 mm.

$\pm 46 \mu\text{m}$ in length and $751 \pm 31 \mu\text{m}$ in width (Figure 5).

Though juvenile hatching was not observed directly, late embryos removed from the egg capsules showed a well-developed foot, which had an oval, thin and transparent operculum on its posterior end. Both cephalic tentacles were well developed. On the left side of the embryos, a long siphon extended from the mantle. No remains of velum were observed on these juveniles, even though the velum was present in earlier embryos removed from other

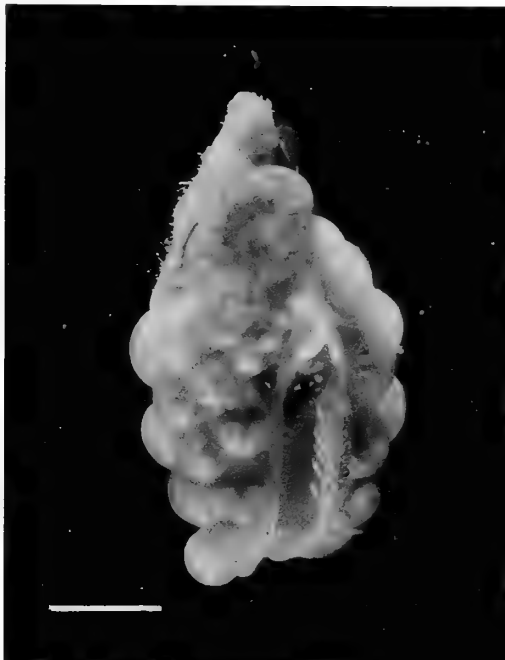


Figure 6

Strombina pumilio (MCNUSB-H144) from Isla Caribe, with egg capsules attached to shell. Scale bar: 5 mm.

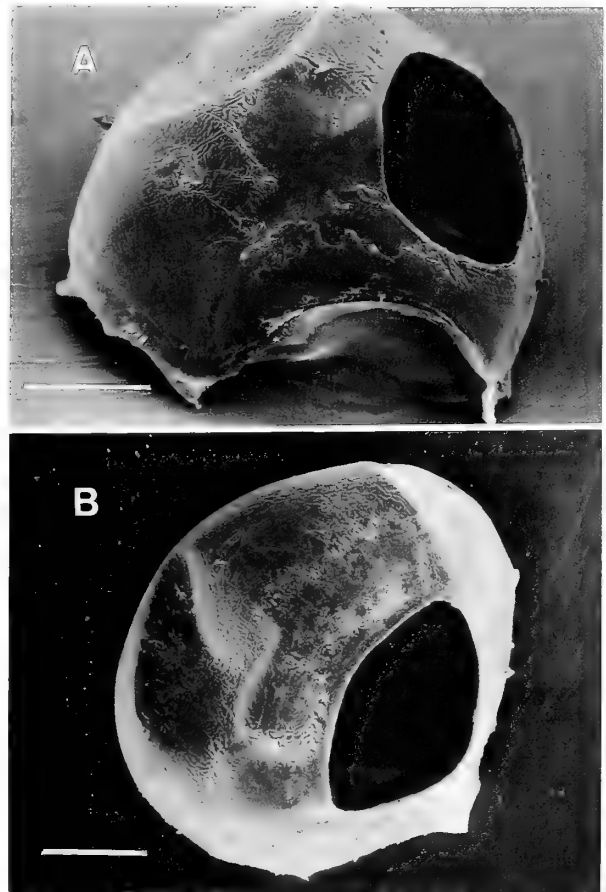


Figure 7

SEM pictures of *Strombina pumilio* egg capsule, from Las Maritas. The membrane of the escape aperture has been removed. A. Side view. B. Top view. Scale bar: 0.5 mm.

egg capsules. These morphological characters indicate that embryos hatch as crawling juveniles.

Strombina pumilio

Adults were found buried or crawling on sandy patches near or among turtle and eel grass beds, in water between 2 to 6 m deep. The observed specimens measured from 18 to 21 mm in length.

Spawns were found in a compact mass covering most of the body whorl, especially around the shell aperture and the last two or three teleoconch whorls (Figure 6). Those attached directly to shell were dome shaped and their base was flat; the other ones, laid over other egg capsules, were irregular at the base, which became concave (Table 1). A narrow, thin and irregular flange surrounded the egg-capsule base. At both sides of the egg capsule, a curved suture on the wall ran longitudinally from one side of the egg capsule to the border of the oval escape aperture. The aperture was formed by the separation of both suture borders and was covered by an opaque membrane, located on one side of the egg-capsule wall (Figure 7A, B). The

Table 2

Number of eggs, developing embryos, and juveniles of *Strombina francesae* and *S. pumilio*. Trocophore stages and early embryos are considered under the column headed *Developing embryos/capsule*. The MCNUSB catalogue number is under the scientific name. Data in parentheses correspond to the number of full egg capsules.

Species	Total number of egg capsules	Uncleaved eggs/capsule	Developing embryos/capsule	Late embryos/capsule
<i>Strombina francesae</i> H266	62	5 (5)	5 (46)	5 (7)
<i>Strombina pumilio</i> H267	15	—	3–5 mode = 5 (12)	5 (1)
<i>Strombina pumilio</i> H217	18	—	3–4 mode = 3 (10)	3–4 mode = 3 (3)
<i>Strombina pumilio</i> H253	26	5 (7)	3–5 mode = 3 (19)	—
<i>Strombina pumilio</i> H144	25	—	4–5 mode = 5 (20)	—

surface of the wall and membrane was covered by numerous short and crossed grooves (Figure 8).

Uncleaved zygotes from seven egg capsules found on one specimen from Isla Caribe (MCNUSB-H253) measured $616 \pm 48 \mu\text{m}$ in diameter (Table 2). Evidence of nurse eggs was not found. Furthermore, undeveloped eggs were not found on egg capsules containing developed embryos,

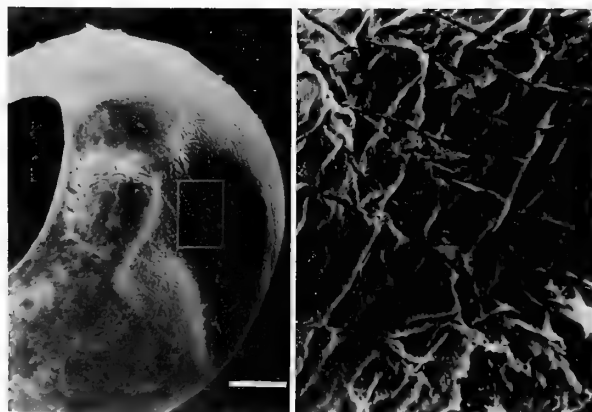


Figure 8

SEM detail of the surface of the egg capsule of *Strombina pumilio*, from Las Maritas. The enclosed area is enlarged on the right side of the figure. Scale bar: 0.25 mm.

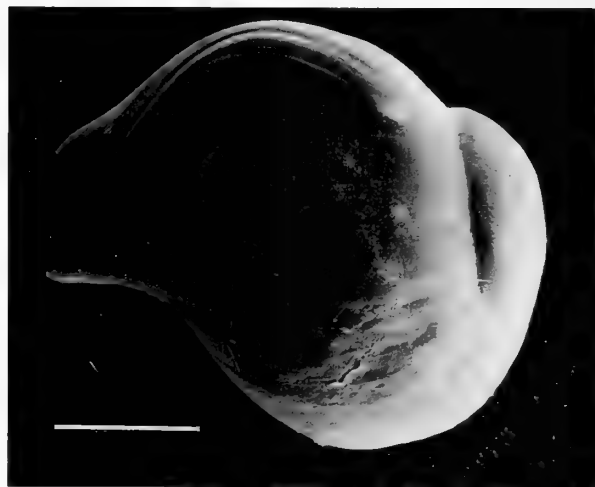


Figure 9

SEM picture of a juvenile shell of *Strombina pumilio* hatched from a spawn collected at Las Maritas. Scale bar: 0.25 mm.

and yolk remains were not found in all the egg cases analyzed.

At hatching, juveniles from Las Maritas showed a well-developed foot and crawled out of the capsule through the escape aperture. A small, elongated, thin and translucent operculum was observed on the posterior end of the foot. Both cephalic tentacles were well formed. No remains of velum were observed on these juveniles or on late embryos removed from egg capsules attached to Isla Caribe specimens. A long siphon was also present. Well-preserved shells of 11 hatchlings from Las Maritas spawn showed from 1.25 to 1.5 whorls and measured $947 \pm 97 \mu\text{m}$ in total length and $855 \pm 91 \mu\text{m}$ in maximum width (Figure 9).

DISCUSSION

Strombina pumilio and *S. francesae* do not seem to be the only species of this genus to use their own shells as a spawning substrate. Roundish egg capsules attached to shells of *Strombina lanceolata* (G. B. Sowerby, 1832) from the Galapagos Islands have been shown by JUNG (1989: 60, fig. 82, pls. 19–21), and other eastern Pacific strombinids seem to follow the same pattern (Dr. Beatrice Moor, unpublished observations). Laying egg capsules on the living shells of its own species seems to be also the most common behavior of the columbellid *Mazatlanica aciculata*, which inhabits sandy beaches along the Venezuelan coast (PENCHASZADEH *et al.*, 1983).

The simple domed egg-capsule pattern has been reported for a number of families like Muricidae, Buccinidae, Nassaridae, Mitridae, and Turridae (THORSON, 1940; BANDEL, 1974). Similar but smaller than *Strombina* egg capsules are those of *Mitrella argus* (Orbigny, 1842) and *Mazatlanica aciculata* (BANDEL, 1974; PENCHASZADEH *et al.*,

1983). Egg capsules of other columbellids that have the same basic shape but are decorated with variable axial ribs and concentric ridges are those of *Columbella mercatoria* (Linné, 1758) and *C. rustica* (Linné, 1758), *Anachis veleda* (Duclos, 1846), *A. pulchella* (Blainville, 1829), *Mitrella ocellata* (Gmelin, 1791), and *Pyrene rosacea* Gould (THORSON, 1935; BACCI, 1947; MARCUS & MARCUS, 1962; BANDEL, 1974). Nevertheless, the most similar egg capsules to those described for *Strombina* spp. seem to be those reported by AMIO (1955) for *Pyrene misera* (G. B. Sowerby, 1844), which seem to have a reticulated wall surface, as in *S. pumilio*, "but fibrous" according to the author, with their exit hole, located near the top of the case, as in *S. francesae*. The relative position of the escape aperture and the morphology of the wall surface are the major differences between egg cases of both *Strombina* species.

Of the 40 columbellid species reviewed, we found 16 in which juveniles hatch from the egg capsules as crawling snails. *Columbella blanda* and *C. rustica* have egg diameters clearly smaller than those reported herein for *Strombina*, 160–180 and 280 μm , respectively (THORSON, 1940; FRANC, 1941; BACCI, 1947), and their embryos feed on nurse eggs to reach full development. An identical pattern of nurse-egg feeding seems to occur in *Anachis avara*, *Columbella mercatoria*, *C. flava*, *Nitidella ocellata*, and *Pyrene misera*, even though the egg diameter of *Pyrene* varies from 315 to 320 μm (PETIT & RISBEC, 1929; PERRY & SCHWENGEL, 1955; AMIO, 1955, 1963; RAEIHLE, 1969; BANDEL, 1974; FLORES, 1978). Although *P. linschkei* (Smith, 1879) have one of the largest uncleaved egg diameters reported in columbellids (390 μm) (AMIO, 1957, 1963), the egg size of the *Strombina* species is almost twice as large, becoming the largest ever reported in this family.

Anachis avara (Say, 1822), reported by FLORES (1978), *A. iontha*, *A. pulchella* (Ravenel, 1861), *Nitidella nitida* (Lamarck, 1822), *Pyrene linschkei*, two unidentified species of *Anachis* (RAEIHLE, 1969; BANDEL, 1974), and two unidentified species of *Columbella* (LEBOUR, 1945; AMIO, 1963) show a lecithotrophic strategy with embryos undergoing intracapsular development, not feeding on nurse eggs, as in both *Strombina* species (AMIO, 1957, 1963; BANDEL, 1974).

ACKNOWLEDGMENTS

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A Review of the Genus *Kaiparathina* Laws, 1941 (Mollusca: Gastropoda: Trochoidea)

by

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Abstract. The genus *Kaiparathina* Laws, 1941, is referred to the trochid subfamily Margaritinae in a new tribe, **Kaiparathinini**. The type species of *Kaiparathina*, *K. praecellens* Laws, 1941 (Early Miocene, New Zealand) is illustrated, *Calliotrochus navakaensis* Ladd, 1982 (Pleistocene, Vanuatu) is referred to the genus, and the following new Recent species are described: *K. boucheti* and *K. vaubani* (New Caledonia), *K. coriolis* (northern Lord Howe Rise), *K. fasciata* (southern Norfolk Ridge), *K. daedala* (Réunion). *Kaiparathina senex* sp. nov. is based on a specimen from the Late Paleocene-Early Eocene of the Chatham Islands, New Zealand.

Kaiparathina species have an extremely distinctive radular morphology and are unique among archaeogastropods in having large, clearly delineated zones of unknown function on each side between the epipodial fringe and the sole. They are evidently sponge-feeders.

INTRODUCTION

Kaiparathina Laws, 1941, was proposed for a distinctive gastropod (*K. praecellens* Laws, 1941) from the richly fossiliferous Early Miocene beds at Pakaurangi Point, Kaipara Harbour, northern New Zealand. Although LAWS (1941) did not specifically refer *Kaiparathina* to any family, the bestowed name and comparative remarks clearly indicate that he considered it to belong to the Janthinidae. BEU (1973) subsequently noted that the type species has a nacreous layer and thus referred it to Trochidae. The present contribution was initiated when I realized that *Calliotrochus navakaensis* Ladd, 1982, and some undescribed Recent species belong in *Kaiparathina*. Recent *Kaiparathina* species occur in the tropical and subtropical Indo-West Pacific on or near rocky substrata at 133–610 m depth (living specimens from rocky ground at 210–610 m).

Abbreviations: AMS—Australian Museum, Sydney; AUG—Auckland University Geology Department; BMNH—The Natural History Museum, London; LACM—Los Angeles County Museum of Natural History; MNHN—Museum National d'Histoire Naturelle, Paris; MNZ—Museum of New Zealand, Wellington; NMP—Natal Museum, Pietermaritzburg; NZGS—Institute of Geological and Nuclear Sciences, Lower Hutt; USNM—National Museum of Natural History, Washington D.C.

SYSTEMATIC TREATMENT

Order Archaeogastropoda Thiele, 1925

Suborder Vetigastropoda Salvini-Plawen, 1980

Superfamily TROCHOIDEA Rafinesque, 1815

Family TROCHIDAE Rafinesque, 1815

Subfamily MARGARITINAE Stoliczka, 1868

Tribe **Kaiparathinini** Marshall, new

Distribution: Late Paleocene-Recent, tropical and subtropical southwest Pacific and Réunion.

Diagnosis: Shell similar to those of Margaritinae, anomphalous, with peripheral keel and sigmoidal labral growth lines on base, spirally sculptured. Snout fringed with papillate processes, prominent propodial horns, no cephalic lappets. Large, swollen, clearly delineated, subcircular anterolateral structures on each side of foot between epipodial fringe and sole. Ctenidium bipectinate, afferent membrane short. Central and lateral radular teeth strongly hooded and flanged, central tooth exceptionally large; shafts of all but innermost and outermost marginal teeth incompletely separated; innermost marginal not enlarged.

Description: Shell conispiral, up to about 10 mm high, thin to rather thick, anomphalous, glossy, nacreous within,

teleoconch frequently with supramedian and peripheral rows of spots and/or wavy axial lines. Protoconch smooth apart from few fine spiral threads. Teleoconch whorls all convex or becoming almost flat, periphery weakly or strongly angulate, base weakly convex or more or less flat; periphery with rounded spiral cord; all spire whorls or first 2 spire whorls spirally liriate; base with or without spiral lirae; collabral growth lines weakly sigmoidal on spire, more strongly sigmoidal on base. Aperture subcircular, peristome discontinuous. Operculum chitinous, multispiral, thin, growing edge short. Animal with prominent papillate processes at broad snout edge. Large swollen, subcircular anterolateral structures on each side of foot between non-digitate epipodial fringe and sole; each anterolateral structure bounded by low ridge, comprising crowded, minutely pustulose, hemispherical structures (histology and function unknown). Epipodial tentacles of moderate size, minutely and densely papillate, numbering 3 on each side; no cephalic lappets, neck lobes simple; prominent propodial horns. Ctenidium large, bipectinate, free tip long and tapered, leaflets on right side thicker, afferent membrane short. Radular teeth in about 40 cross rows, central field evenly curved; central and lateral teeth stout, with angulate, strongly hooded cutting areas, shafts laterally flanged and grooved, faces thickened, central tooth relatively large; lateral teeth multiplying by progressive in-column morphological transformation of marginal teeth into a late stage of ontogenesis, smoothly enlarging outwards, 4–9 pairs per cross row at maturity; no latero-marginal plates; marginal fields narrow, teeth numerous, morphologically grading rather smoothly into laterals, slender, tips rounded and finely serrate, outermost marginal much broader than inner marginals, shafts of all but innermost and outermost teeth incompletely separated. Jaws present.

Remarks: Although undoubtedly trochoidean, species of *Kaiparathina* cannot be satisfactorily grouped into any of the known families or subfamilies as defined by HICKMAN & MCLEAN (1990). Among Trochoidea, the topographically complex, strongly hooded, laterally interlocking teeth of the central radular field are most similar to those in adult Eucyclinae, especially Calliotropini (HICKMAN & MCLEAN, 1990:figs. 43, 47), the radula differing principally by having a relatively larger central tooth, and incompletely separated marginal teeth with broad comblike cutting areas. The ctenidium most closely resembles those in Eucyclinae, Margaritinae, and Tegulinae, which differ markedly from those of other trochid subfamilies (HICKMAN & MCLEAN, 1990). This ctenidial type—fully bipectinate with a long free tip and a short afferent membrane—is characteristic of trochoideans with particularly long fossil records, and has been interpreted by HICKMAN & MCLEAN (1990) as a plesiomorphy. *Kaiparathina* seems unlikely to be closely related to Eucyclinae, in which the shell sculpture is predominantly axial, especially on the early teleoconch whorls, while the heavy shells of the lit-

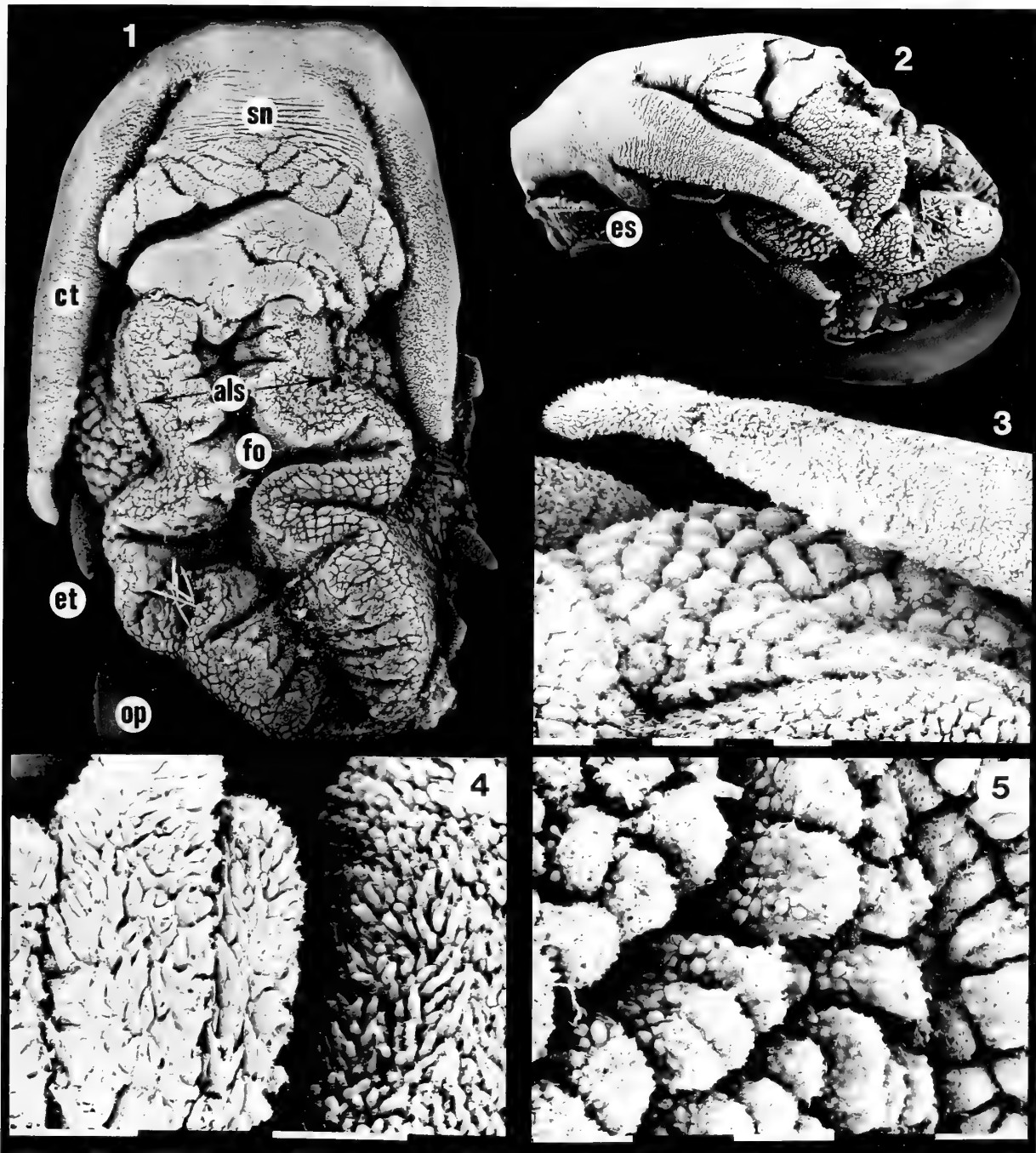
toral or shallow sublittoral Tegulinae are entirely dissimilar. Among the three subfamilies, shell morphology most closely approaches that of Margaritinae, in which spiral sculpture is also predominant, if not on all teleoconch whorls then usually on the earliest ones. Although probably independently derived, some aspects of head-foot morphology approach those exhibited by *Gaza superba* (Dall, 1881) (Margaritinae, Gazini) in which the edge of the oral shield is digitate, and the foot has anterolateral projections. *Gaza superba* is, however, strongly dissimilar in size and in shell and adult radular morphology, and in other aspects of head-foot morphology (HICKMAN & MCLEAN, 1990).

The central and lateral radular teeth of all known adult margaritines differ from those in *Kaiparathina* by having strongly outwardly bowed shafts, broader and flatter shaft faces, and non-hooded cutting areas (HICKMAN & MCLEAN, 1990:figs. 50, 53). As shown by WARÉN (1990), trochoidean radulae undergo often profound progressive morphological transformations during ontogenesis, and the radulae of most juvenile trochoideans (with the notable exception of calliostomatids) are at first essentially similar to each other. For this reason it is unnecessary to invoke progressive “horizontal” evolutionary transformations to derive divergent radular morphologies from one another. Since adult radulae of *Kaiparathina* species are not unlike those of juvenile trochoideans in general (WARÉN, 1990), it would seem that somatic development of their radulae is retarded (paedomorphosis) relative to that in Margaritinae, Eucyclinae, and Tegulinae. This contention is supported by the relatively narrow marginal fields with relatively low numbers of incompletely separated teeth.

Accordingly, and despite the differences in adult radulae, I conclude that *Kaiparathina* and Margaritinae are related. While this group may well prove worthy of subfamilial status on the basis of additional data (e.g., anatomical and molecular), for the present I regard it as a clade within Margaritinae, for which the informal tribal name **Kaiparathinini** is introduced.

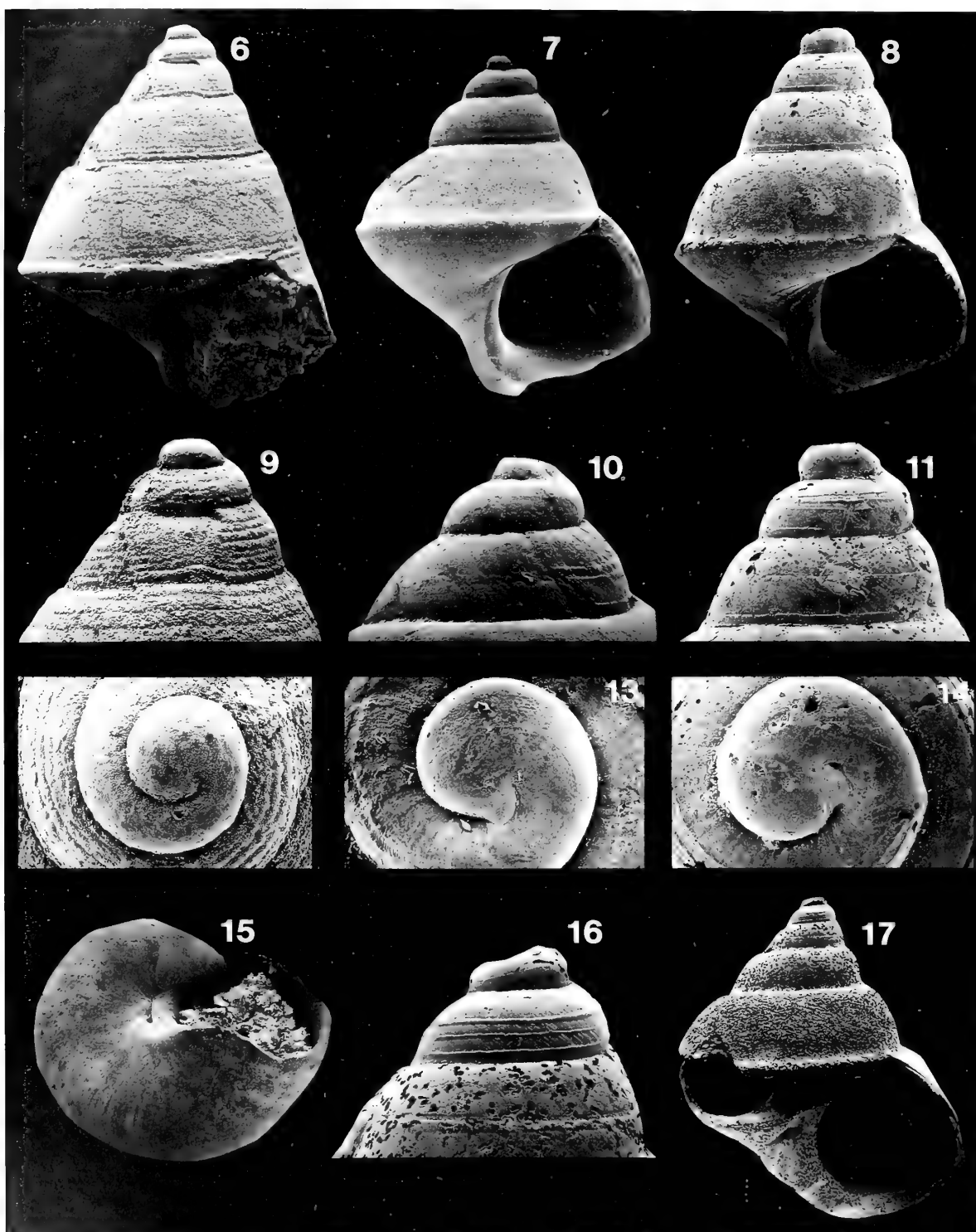
Intestinal tracts of specimens of *Kaiparathina boucheti* contain much fine, white matter of unknown origin together with numerous minute, silicious sponge spicules, predominantly tetraxonic. That these spicules are the remains of prey rather than incidentally ingested components of detritus is suggested not only by their quantity but also by the large size and morphology of the central radular tooth, which seems to be ideally suited for prey penetration and slicing rather than for detritivory or deposit feeding. Sponge feeding is rare among Trochoidea and is known only in a few species of Calliostomatidae (summarized by MARSHALL, 1988) and in at least some of the Trochacrididae (HAIN, 1990; HICKMAN & MCLEAN, 1990; personal observations).

The anterolateral fields on the sides of the foot are a radical departure from the standard trochoidean plan and are clearly apomorphic (Figures 1–3, 5). Their function is unknown.



Explanation of Figures 1 to 5

Figures 1–5. *Kaiparathina boucheti* Marshall, sp. nov. Critical-point dried animal (retracted, unfixed, *ex* alcohol), MUSORSTOM 4 sta. DW221. Figures 1–2. Head-foot, subject length 4.8 mm; note prominent propodial horns inclined to animal's left in Figure 1. Figure 3. Detail of tip of right cephalic tentacle and ventral margin of right anterolateral structure. Figure 4. Detail of dorsal surface of right cephalic tentacle (right) and tentaculiform processes at snout edge. Figure 5. Detail of right anterolateral structure showing granulate surface. als, anterolateral structure; ct, cephalic tentacle; es, eyestalk; et, epipodial tentacle; fo, foot; op, operculum; sn, snout. Scales = 100 μ m.



Explanation of Figures 6 to 17

Figures 6-17. *Kaiparathina* species.

Figures 6, 9, 12. *K. senex* Marshall, sp. nov., holotype, Late Paleocene-Early Eocene, Pitt Island, Chatham Islands, New Zealand, shell height 3.90 mm. Detail width in Figure 9 = 1.60 mm, Figure 12 = 970 μ m.

Figures 7, 10, 13, 15. *K. praecellens* Laws, 1941, Early Miocene, Pakaurangi Point, Kaipara Harbour, New

Genus *Kaiparathina* Laws, 1941

Kaiparathina LAWS, 1941:145. Type species (by original designation): *Kaiparathina praecellens* Laws, 1941; Early Miocene, Pakaurangi Point, Kaipara Harbour, New Zealand.

Diagnosis and Description as for *Kaiparathinini*.*Kaiparathina praecellens* Laws, 1941

(Figures 7, 10, 13, 15)

Kaiparathina praecellens LAWS, 1941:145, pl. 19, fig. 38; FLEMING, 1966:49; JONES, 1970:164; BEU, 1973:320, figs. 19, 20; BEU & MAXWELL, 1990:404.

Type data: Holotype NZGS TM 1400: Pakaurangi Point, Kaipara Harbour, New Zealand; Otaian (Early Miocene).

Other material examined: (7 specimens MNZ, 10 NZGS). Tuffaceous siltstone, small bay ca. 1.6 km NW of Pakaurangi Point, Kaipara Harbour, New Zealand, map ref. Q8/262513 (f 9828), March 1979, B. A. Marshall and P. A. Maxwell; Otaian (Early Miocene).

Distribution: Early Miocene (Otaian), Pakaurangi Point, Kaipara Harbour, northern New Zealand.

Remarks: As noted by LAWS (1941) some specimens retain traces of the original color pattern, which is evidently restricted to the last adult whorl; it comprises wavy axial lines that extend abapically from about midway between the suture and periphery and across the base. The lines are gently opisthocline on the spire, and so strongly opisthocline as to be almost spiral on the base. A somewhat similar color pattern is exhibited by *Kaiparathina navakaensis* (Ladd, 1982) and *K. vaubani* sp. nov. (Figure 27). JONES (1970) concluded that beds containing *K. praecellens* were deposited in a warm sea at up to about 250 m depth.

Kaiparathina senex Marshall, sp. nov.

(Figures 6, 9, 12)

Description: Shell (holotype) 3.90 mm high, higher than broad, spire 1.5× as high as aperture, of moderate thickness, anomphalous.

Protoconch 430 µm wide, surface etched away.

Teleoconch of 4.4 whorls. First 1.5 whorls evenly convex, subsequent whorls weakly convex, periphery angulate, base more or less flat. First whorl with 5 rounded, closely spaced spiral cords, multiplying to 10 on subsequent whorls, peripheral spiral strongest, rounded, others broad

and flattened with sublinear interspaces. Base with 15 similar, rounded spiral cords with interspaces about as wide as each spiral. Collabral growth lines prosocline on spire, sigmoidal on base. Aperture subquadrate, outer lip thin, inner lip thick.

Type data: Holotypes NZGS TM 7301, GS 12159 (CH/f471), Coarse Red Bluff Tuff on large wave-cut platform and in low outcrops at base of cliff below Pliocene section on cliff due north of The Bluff homestead (grid ref. NZMS 260/234712), Pitt Island, Chatham Islands, New Zealand, Jan. 1977, A. G. Beu, P. A. Maxwell and H. J. Campbell: Late Teurian-Early Waipawan (Late Paleocene-Early Eocene).

Distribution: Late Paleocene-Early Eocene (Late Teurian-Early Waipawan), Pitt Island, Chatham Islands, New Zealand.

Remarks: *Kaiparathina senex* differs from all other species of *Kaiparathina* by having a larger protoconch, and more numerous and persistent spiral cords on the spire. *Kaiparathina daedala* sp. nov. has a similar number of weaker spiral cords on the base.

According to BEU & MAXWELL (1990:88) the Red Bluff Tuff faunules inhabited a hard substratum on the summits or flanks of volcanic sea-mounts in an oceanic environment, probably at outer shelf or bathyal depths.

Etymology: Old (Latin).

Kaiparathina navakaensis (Ladd, 1982)

(Figures 8, 11, 14, 27; Table 1)

Calliotrochus navakaensis LADD, 1982:24, pl. 34, figs. 9–11.

Type data: Holotype, USNM 214405: United States Geological Survey loc. 24198, Navaka River, Santo, Vanuatu; Pleistocene.

Other material examined: 1 topotype USNM.

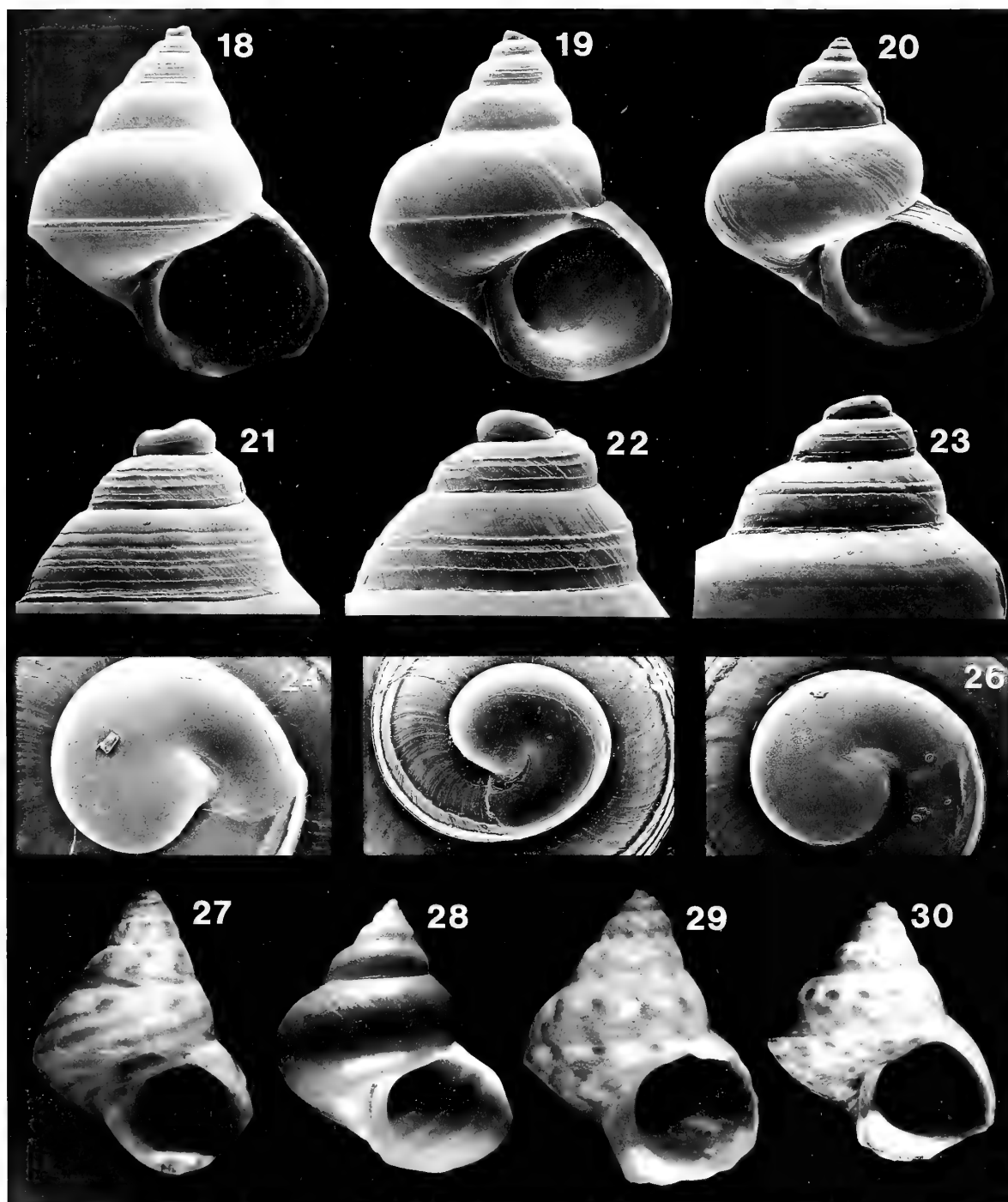
Distribution: Pleistocene, Santo, Vanuatu.

Remarks: Although originally referred to the genus *Calliotrochus* Fischer, 1879 (type species *Turbo phasianellus* Deshayes, 1863), Ladd's species clearly belongs in *Kaiparathina*. The type species of *Calliotrochus* (DESHAYES, 1863:pl. 36, figs. 13, 14; WENZ, 1938:fig. 620) differs markedly in shell facies and the genus apparently belongs in subfamily Trochinae, tribe Gibbulini (HICKMAN & MCLEAN, 1990). From the Recent species described here-

← Zealand, NZGS TM 7303. Figure 7. Shell height 2.30 mm. Detail width in Figure 10 = 900 µm, Figure 13 = 470 µm, Figure 15 shell width = 3.20 mm.

Figures 8, 11, 14. *K. navakaensis* Ladd, 1982, Pleistocene, Santo, Vanuatu, USNM 459658, shell height 2.05 mm. Detail width Figure 11 = 950 µm, Figure 14 = 480 µm.

Figures 16, 17. *K. sp. cf. navakaensis* Ladd, 1982, MUSORSTOM 6 sta. DW410, off Lifou, Loyalty Islands, 490 m, MNHN, shell height 5.00 mm. Detail width in Figure 16 = 1.30 mm.



Explanation of Figures 18 to 30

Figures 18–30. *Kaiparathina* species.

Figures 18, 21, 24. *K. boucheti* Marshall, sp. nov., holotype, BIOCAL sta. DW46, off southern New Caledonia, 570–610 m, shell height 5.45 mm. Detail width in Figure 21 = 1.60 mm, Figure 24 = 530 μ m.

Figures 19, 22, 25. *K. vaubani* Marshall, sp. nov., holotype, MUSORSTOM 4 sta. DW164, off northern New Caledonia, 255 m, shell height 3.70 mm. Detail width in Figure 22 = 1.00 mm, Figure 25 = 500 μ m.

Figures 20, 23, 26, 28. *K. coriolis* Marshall, sp. nov., holotype, MUSORSTOM 5 sta. 309, Nova Bank, northern Lord Howe Rise, 340 m, shell height 10.1 mm. Detail width in Figure 23 = 1.70 mm, Figure 26 = 500 μ m.

Table 1

Kaiparathina navakaensis and *K. sp. cf. navakaensis*. Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls	Material
5.00	4.90	1.02	4.60	DW410
4.90	4.40	1.11	4.75	DW410
3.90	3.25	1.20	4.60	Holotype
2.95	2.75	1.07	3.70	DW08
2.05	1.75	1.17	3.50	Paratype

in, the holotype of *K. navakaensis* is distinguished by its very thick shell, the weakly convex 2nd–4th teleoconch whorls, and the color pattern of dark, strongly opisthocline bands that are continuous across the spire and base. A topotype (Figures 8, 11, 14) resembles the holotype in shell thickness and sculpture, but differs by having a smaller protoconch (width 330 μ m instead of 370 μ m) and less markedly flattened teleoconch whorls. The specific status of this topotype cannot be resolved with such limited material, and it is only tentatively interpreted as *K. navakaensis*.

Kaiparathina navakaensis may still be living off Vanuatu, and perhaps off the Loyalty Islands as well (see below).

Kaiparathina sp. cf. navakaensis (Ladd, 1982)

(Figures 16, 17; Table 1)

Material examined: (3 specimens MNHN): BIOCAL sta. DW08, 20°34'S, 166°54'E, off Lifou, Loyalty Is., dead, 435 m, n.o. *Jean-Charcot* (1); MUSORSTOM 6 sta. DW410, 20°38'S, 167°07'E, off Lifou, dead, 490 m, n.o. *Alis* (2).

Remarks: Three specimens dredged off Lifou, Loyalty Islands closely resemble the holotype of *Kaiparathina navakaensis* (Figure 27) in shell shape, sculpture, and thickness. They differ primarily by having slightly broader protoconchs (width 400 μ m instead of 370 μ m holotype and 330 μ m in topotype). Although all three are bleached and etched to some extent, the late teleoconch whorls of the two shells from station DW410 have a pale, dull, pinkish flush, and one has darker peripheral blotches. Additional, better preserved material from both Vanuatu and the Loyalty Islands will be required to ascertain the specific status of this form.

Kaiparathina sp. cf. navakaensis and *K. boucheti* occurred together as shells at station DW08.

Table 2

Kaiparathina boucheti Marshall, sp. nov. Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls	Material
6.30	6.10	1.03	4.60	Paratype DW221
5.90	5.40	1.09	4.80	Paratype DW221
5.45	4.75	1.15	4.50	Holotype DW46
4.85	4.20	1.15	4.30	Paratype DW46
4.65	4.05	1.15	4.30	Paratype DW46
4.10	3.55	1.15	4.10	Paratype DW46

Kaiparathina boucheti Marshall, sp. nov.

(Figures 1–5, 18, 21, 24, 39–44; Table 2)

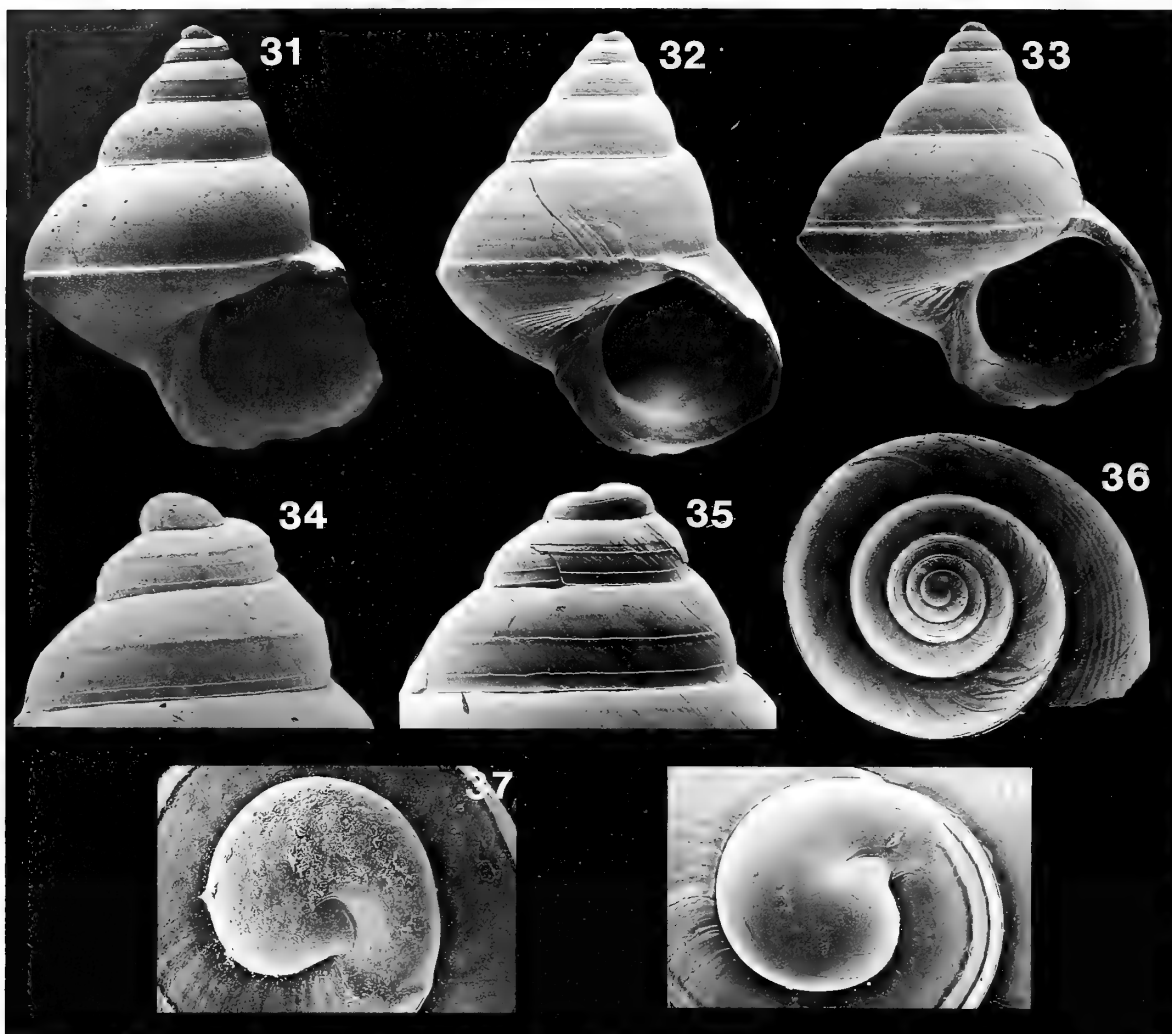
Description: Shell up to 6.30 mm high, slightly higher than broad, spire about as high as aperture, thin, translucent, glossy, anomphalous. Protoconch reddish brown. Start of 1st teleoconch whorl reddish brown, rapidly fading, uniformly nacreous through colorless outer shell layer after 1st 0.5–0.75 whorl.

Protoconch 400–420 μ m wide, with 4 fine, crisp, widely spaced spiral threads.

Teleoconch of up to 4.8 convex whorls, periphery weakly angulate, base gently rounded. First 2 whorls with crisp spiral threads that multiply by intercalation, spirals absent from adapical quarter, abapical (peripheral) threads persisting throughout, others weakening and vanishing on third whorl; spiral threads numbering 3 or 4 at start of 1st whorl, multiplying to 6–8, narrow with broader interspaces on 1st whorl, after which broader with considerably narrower interspaces; abapical spiral gradually enlarging to form rounded peripheral spiral cord. Base with or without 1 or 2 spiral threads close beside peripheral spiral and columella; obscure spiral lines throughout. Aperture subcircular, outer lip thin, inner lip thick, parietal glaze very thin. Collabral growth lines prosocline on spire, sigmoidal on base.

Animal (Figures 1–5) milky white. Snout tip broadly expanded, with prominent papillate processes. Cephalic tentacles large, dorsoventrally flattened, tapered, minutely and densely papillate, large eyes at tips of swollen outer basal eyestalks; neck lobes thin, not digitate, right considerably larger than left; epipodial tentacles of moderate size, minutely and densely papillate, 3 on each side; no cephalic lappets; large, swollen, clearly demarcated anterolateral structures between epipodial fringe and sole; foot large,

Figures 27–30. Photographs of uncoated shells to show color patterns. Figure 27. *K. navakaensis*, Ladd, 1982, holotype, shell height 3.90 mm. Figure 28. *K. coriolis* Marshall, sp. nov., holotype, shell height 10.1 mm. Figure 29. *K. fasciata* Marshall, sp. nov., holotype, shell height 3.35 mm. Figure 30. *K. daedala* Marshall, sp. nov., paratype (MNHN), shell height 4.05 mm.



Explanation of Figures 31 to 38

Figures 31–38. *Kaiparathina* species.

Figures 31, 34, 37. *Kaiparathina fasciata* Marshall, sp. nov., holotype, Wanganella Bank, southern Norfolk Ridge, 133 m, shell height 3.35 mm. Detail width in Figure 34 = 1.00 mm, Figure 37 = 460 μ m.

Figures 32, 33, 35, 36, 38. *Kaiparathina daedala* Marshall, sp. nov. Figures 32, 35, 38. Holotype, off Réunion, 210–227 m, shell height 4.65 mm. Detail width in Figure 35 = 1.40 mm, Figure 38 = 470 μ m. Figures 33, 36. Paratype (MNHN), off Réunion, 280–340 m, shell height 4.05 mm, width 3.80 mm.

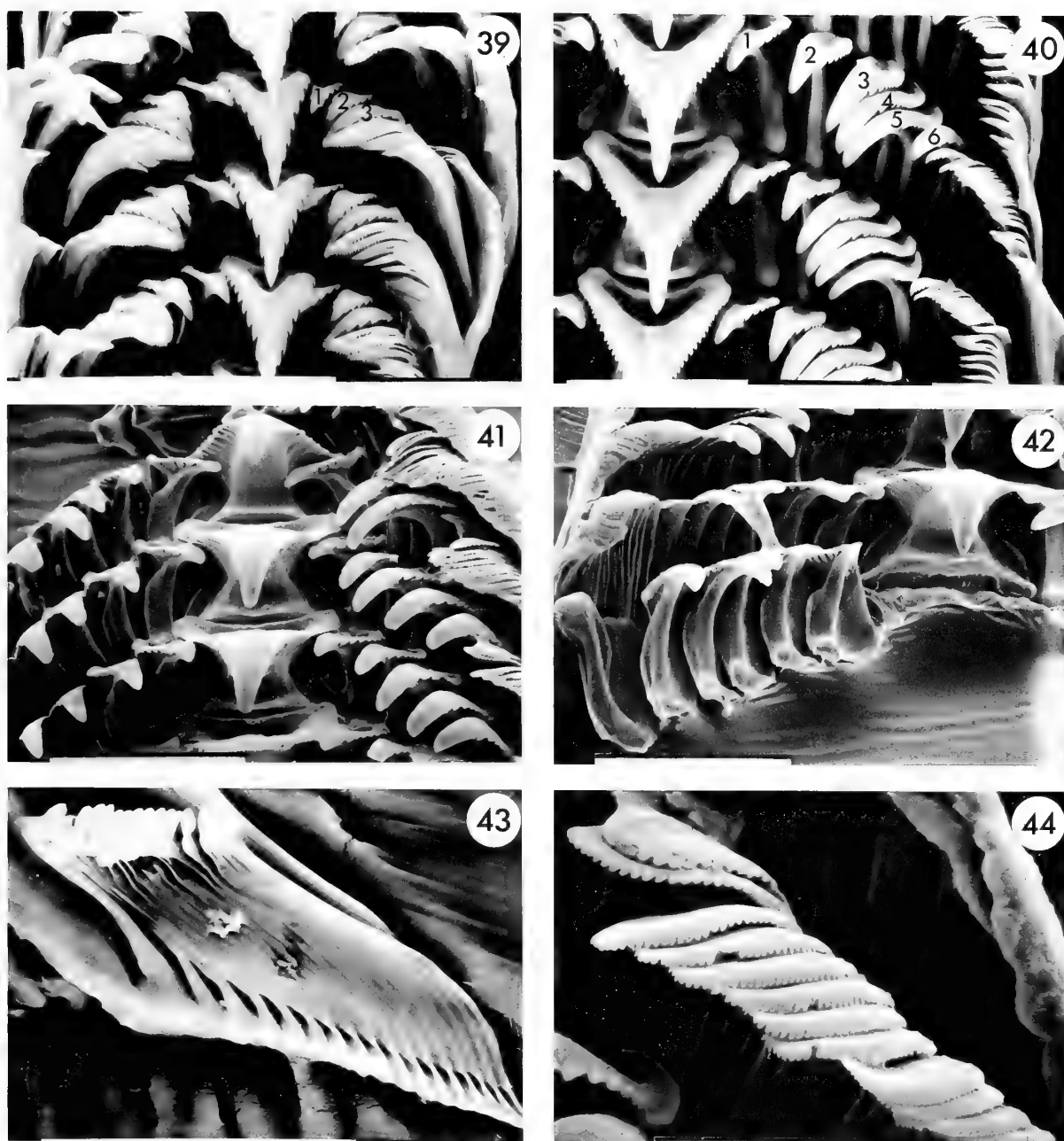
elongate, with prominent anterior horns, posteriorly tapered. Operculum rather thin, chitinous, multispiral, growing edge short.

Radula (Figures 39–44) with the formula $\infty + 6 + 1 + 6 + \infty$. Central tooth large, very stoutly built, about as long as broad; cutting area narrowly angulate, strongly hooked, laterally flanged, edges finely serrate; terminal cusp large, slender; shaft face strongly thickened, back concave; base laterally flanged to interlock with lateral teeth. Lateral teeth progressively multiplying to 6 pairs by in-column transformation of marginals, longer than broad, elongating outwards, stout; cutting areas laterally flanged, narrowly tapered, finely serrate, terminal cusp large; shaft face strongly thickened, outer edge modestly flanged and

inner edge very strongly flanged to interlock with adjacent teeth. Marginal teeth numerous; outermost tooth broad and laminar, inner teeth slender, tips blunt, finely serrate, shafts of all but innermost and outermost teeth incompletely separated.

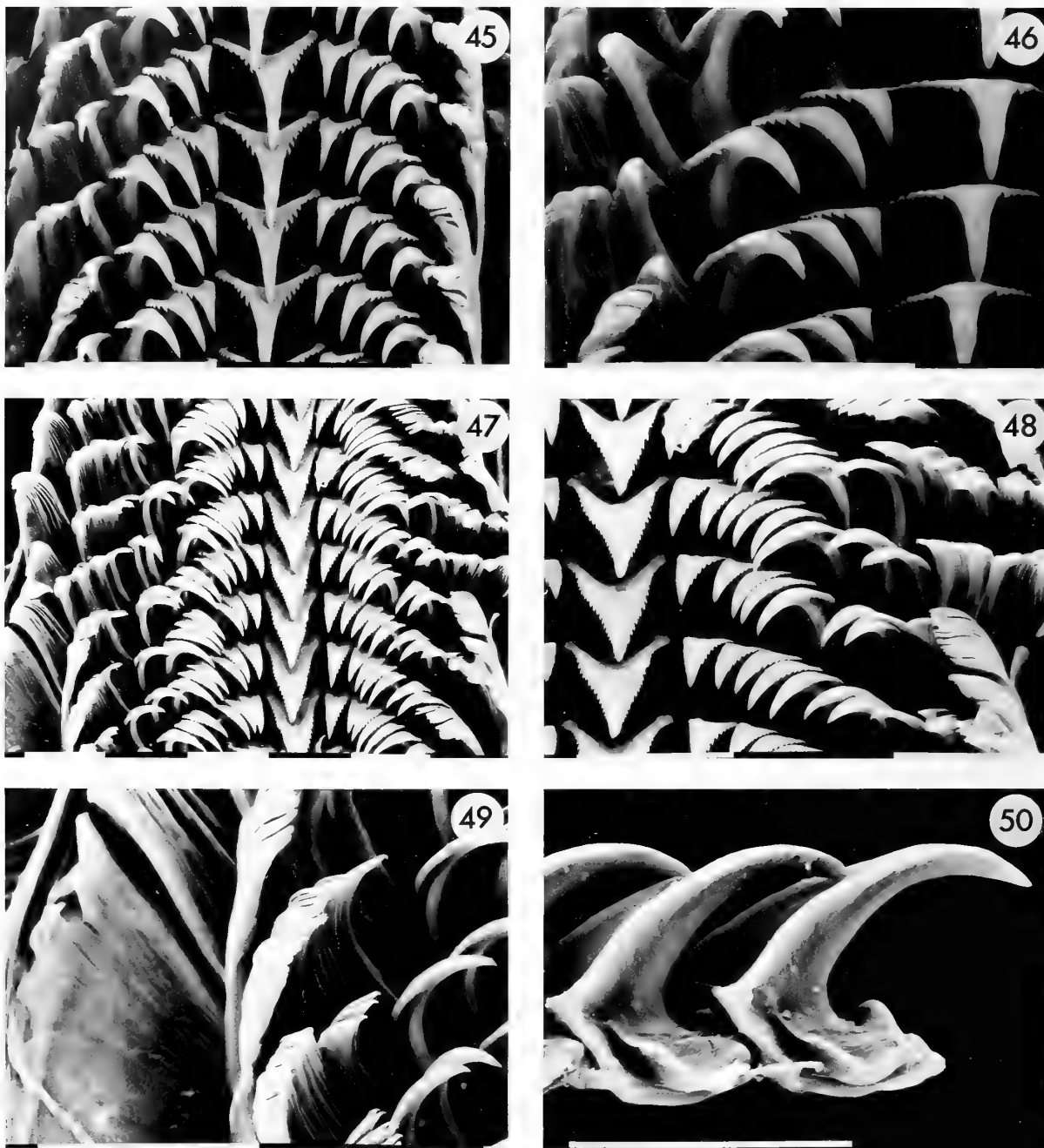
Jaw plates like those in *Kaiparathina coriolis* and *K. daedala* (see below).

Type material: Holotype MNHN, and 4 paratypes (3 MNHN, 1 MNZ): BIOCAL sta. DW46, 22°53'S, 167°17'E, off S New Caledonia, alive, 570–610 m, n.o. *Jean-Charcot*. Paratypes (39): MUSORSTOM 4 sta. DW 151, 19°07'S, 163°22'E, dead, 200 m, n.o. *Vauban* (1 MNHN); BIOCAL sta. DW08, 20°54'S, 166°54'E, dead,



Explanation of Figures 39 to 44

Figures 39–44. *Kaiparathina boucheti* Marshall, sp. nov., radulae. Figure 39. Entire width of radula from juvenile paratype, shell height 2.60 mm, showing 3 pairs of lateral teeth, MUSORSTOM 4 sta. DW221 (MNHN). Figure 40. Part width of radula from adult paratype, shell height 3.65 mm, showing 6 pairs of lateral teeth, MUSORSTOM 4 sta. DW221 (MNHN). Figures 41, 42, 44. Radula *ex* holotype. Figures 41, 42. Details of central and lateral teeth; note laterally flanged cutting areas, massive central tooth, and strongly laterally flanged shafts of lateral teeth. Figure 43. Bank of marginal teeth (lacking outermost tooth at right) from radula illustrated in Figure 44. Figure 44. Tips of inner marginal teeth. Scales Figures 39–43 = 100 μ m, Figure 44 = 25 μ m.



Explanation of Figures 45 to 50

Figures 45, 46. *Kaiparathina vaubani* Marshall, sp. nov., holotype radula. Figure 45. Entire width. Figure 46. Detail of central (right) and lateral teeth.

Figures 47–50. *Kaiparathina coriolis* Marshall, sp. nov., holotype radula. Figure 47. Entire width. Figure 48. Detail of central and lateral teeth. Figure 49. Detail of outermost lateral (right) and marginal teeth; note broad outermost marginal at lower left and incomplete separation of shafts of teeth above it. Figure 50. Side view of isolated column of central teeth showing the huge cutting area and short basal plate with interlocking lateral flanges and strong median boss. Scales = 100 μ m.

435 m, n.o. *Jean-Charcot* (8 MNHN); BIOCAL sta. DW 83, 20°35'S, 166°54'E, dead, 460 m, n.o. *Jean-Charcot* (1 MNHN); BIOGEOCAL sta. DW307, 20°35'S, 166°55'E, dead, 470–480 m, n.o. *Coriolis* (1 MNHN); BIOCAL sta. KG 06, 20°36'S, 166°53'E, dead, 735 m, n.o. *Jean-Charcot* (1 MNHN); MUSORSTOM 4 sta. DW225, 22°52'S, 167°23'E, dead, 590–600 m, n.o. *Vauban* (1 MNHN); BIOCAL sta. CP 40, 22°55'S, 167°24'E, dead, 650 m, n.o. *Jean-Charcot* (1 MNHN); MUSORSTOM 4 sta. DW222, 22°56'S, 167°33'E, alive, 410–440 m, n.o. *Vauban* (2 MNHN); MUSORSTOM 4 sta. DW221, 22°59'S, 167°37'E, alive, 535–650 m, n.o. *Vauban* (25: 1 AMS, 1 BMNH, 19 MNHN, 2 MNZ, 1 NMP, 1 USNM); SMIB 4 sta. DW61, 23°00'S, 167°22'E, alive, 520–550 m, n.o. *Alis* (1 MNHN); BIOCAL sta. DW56, 23°35'S, 167°12'E, dead, 695–705 m, n.o. *Jean-Charcot* (1 MNHN).

Distribution: Off northern and southern New Caledonia and northern Norfolk Ridge, 200–735 m, living at 410–610 m.

Remarks: *Kaiparathina boucheti* differs from *K. praelans* and *K. navakaensis* by having a thinner shell, a larger protoconch, and more strongly convex teleoconch whorls. *Kaiparathina boucheti* differs further by being more strongly and extensively sculptured on the early teleoconch whorls, by constantly lacking a color pattern, and by being larger relative to the number of whorls (Tables 1, 2).

Etymology: Named after Philippe Bouchet (MNHN).

Kaiparathina vaubani Marshall, sp. nov.

(Figures 19, 22, 25, 45, 46; Table 3)

Description: Shell up to 4.5 mm high, higher than broad, spire about as high as aperture, stout, glossy, anomphalous. Protoconch pinkish to blackish brown. First whorl chocolate on adapical half, or 1st half whorl with pinkish subsutural zone, elsewhere translucent white. Subsequent whorls translucent white, internal nacreous layer showing through thin outer shell layers, with or without narrow, dull pink, opisthocline axial bands on 3rd whorl only, or on 3rd and subsequent whorls, including base. Inner lip white.

Protoconch 330 μ m wide, with 3 fine, crisp spiral threads, otherwise smooth.

Teleoconch of up to 4.75 convex whorls, periphery broadly rounded at maturity, weakly angulate before, base weakly convex. Peripheral keel narrow, rounded, adapical margin shelved and exposed on spire. First 2 spire whorls with 3 similar, narrow, rounded spiral threads on abapical half, their adapical margins sharply shelved, becoming obsolete at end of 2nd whorl. Subsequent whorls smooth apart from obscure spiral and collabral growth lines. Base with a spiral thread beside inner lip. Collabral growth lines prosocline, very weakly sigmoidal on spire, more deeply sigmoidal on base. Aperture subcircular, peristome

Table 3

Kaiparathina vaubani Marshall, sp. nov. Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleo- conch whorls	Material
4.50	3.95	1.14	4.75	Paratype CC175
4.00	3.60	1.11	4.25	Paratype CC175
3.85	3.50	1.10	4.20	Paratype DW38
3.70	3.30	1.12	4.25	Holotype DW164
2.60	2.45	1.06	3.20	Paratype DW38

discontinuous; outer lip thin at rim, thicker and simple within; inner lip thick, parietal gaze very thin.

Animal white, as in *Kaiparathina boucheti* but with longer, more narrowly tapered epipodial tentacles. Operculum as in *K. boucheti*. Jaw as in *K. coriolis* and *K. daedala*.

Radula (Figures 45, 46) similar to that of *Kaiparathina boucheti* but with 4 lateral teeth, a much longer terminal cusp on central tooth, and sharper cusps on lateral teeth.

Type data: Holotype MNHN: MUSORSTOM 4 sta. DW164, 18°33'S, 163°13'E, off d'Entrecasteux Reefs, N New Caledonia, alive, 255 m, n.o. *Vauban*. Paratypes (2): MUSORSTOM 4 sta. CC 175, 18°59'S, 163°17'E, off Grande Récif de Cook, N New Caledonia, dead, 355 m, n.o. *Vauban* (1 MNHN, 1 MNZ).

Other material examined: (2 specimens MNHN): BIOCAL sta. DW38, 23°00'S, 167°15'E, off Grand Récif du Sud, S New Caledonia, dead, 360 m, n.o. *Jean-Charcot*.

Distribution: Northern and southern New Caledonia, 255–360 m, living at 255 m.

Remarks: *Kaiparathina vaubani* differs from *K. navakaensis* and *K. sp. cf. navakaensis* by having a substantially thinner shell, slightly but distinctly stronger sculpture on the first teleoconch whorl, and more strongly convex teleoconch whorls. Some specimens, including the holotype, resemble the holotype of *K. navakaensis* in color pattern, but the color bands in *K. vaubani* are narrower. It differs from *K. boucheti* by having a thicker shell, a smaller protoconch, by usually having axial color bands, and in details of radular morphology.

Etymology: Named after n.o. *Vauban*, with which the type material was obtained.

Kaiparathina coriolis Marshall, sp. nov.

(Figures 20, 23, 26, 28, 47–50, 55, 56; Table 4)

Description: Shell up to 10.1 mm high, slightly higher than broad, spire 0.74 (subadult) to 1.20 \times as high as aperture, stout, glossy, a narrow crescentic umbilical chink

Table 4

Kaiparathina coriolis Marshall, sp. nov. Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls	Material
10.1	9.40	1.07	5.50	Holotype
9.60	8.80	1.09	5.50	Paratype
8.20	8.10	1.01	5.10	Paratype

at maturity. Protoconch white. Teleoconch buff to pale pinkish buff, suprmedian spiral on 1st 3 whorls and exposed part of peripheral keel on 1st 3.5 whorls alternately spotted white and reddish brown. Inner lip and base close beside it white, interior nacreous.

Protoconch 400 μ m wide, 2 fine crisp spiral threads, otherwise essentially smooth.

Teleoconch of up to 5.5 strongly convex whorls; periphery evenly rounded at maturity, weakly angulate before; base weakly convex. Peripheral keel rounded, almost entirely exposed on spire, becoming obsolete late on 5th whorl. Early whorls with rounded suprmedian and suprasutural spiral threads, the latter close beside peripheral keel. Suprmedian spiral becoming obsolete late on 3rd whorl, narrow at first, gradually widening, bounded by grooves; adapical groove narrow throughout; abapical groove as broad as thread on 1st whorl, then progressively infilled by widening spiral thread. Suprasutural spiral bounded adapically by fine groove, becoming obsolete late on 2nd whorl. Elsewhere smooth apart from fine collabral growth lines, prosocline and shallowly sigmoidal on spire, more deeply sigmoidal on base. Aperture subcircular; outer lip thin at rim, thicker and simple within; inner lip thick, parietal glaze thin.

Animal creamy white. Head broad, dorsoventrally flattened. Snout tip concave in front, fringed with prominent, finely and densely papillate projections. Cephalic tentacles tapered, dorsoventrally flattened, minutely and densely papillate, well-developed eyes in prominent eyestalks at outer bases. Neck lobe on right considerably longer than broad, thin, extending from base of eyestalk, none on left. Epipodial fringe prominent, 1 tapered epipodial tentacle on either side, 1 or 2 smaller tentacles on each side of opercular lobe. Anterolateral fields very large, clearly delineated. Foot longer than broad, anteriorly indented between prominent, tapered lateral horns. Operculum thin, chitinous, multispiral.

Jaws (Figures 55, 56) thin, subrectangular with rounded corners, elements minute.

Radula (Figures 47–50) with the formula $\infty + 9 + 1 + 9 + \infty$, 40 cross rows, teeth longer than broad. Central tooth relatively large, stout; cutting area large, laterally flanged, narrowly angulate, curved, sharply serrate; shaft face strongly thickened, shaft back concave; base flanged and grooved to interlock with laterals. Lateral teeth con-

siderably narrower than central; cutting areas narrowly angulate, outer edges laterally flanged and sharply serrate; shaft faces thickened, basal edges flanged and grooved to interlock with adjacent teeth. Marginal teeth slender, cutting areas rounded, leading edges finely serrate, shafts of all but innermost and outermost teeth incompletely separated, outermost few pairs with very broad laminar shafts and smooth tips; innermost tooth morphologically intermediate between inner laterals and outer marginals.

Type material: Holotype and paratype MNHN, paratype MNZ: MUSORSTOM 5 sta. 309, 22°10'S, 159°23'E, Nova Bank, alive, 340 m, n.o. *Coriolis*.

Distribution: Nova Bank, northern Lord Howe Rise, 340 m.

Remarks: *Kaiparathina coriolis* differs from other species of *Kaiparathina* by attaining much larger size, and by details of teleoconch microsculpture, color, and color pattern. It differs further from *K. boucheti* and *K. vaubani* by having more numerous lateral teeth and by details of tooth morphology, particularly the presence of a relatively much smaller terminal cusp on the central tooth.

Etymology: After n.o. *Coriolis*.

Kaiparathina fasciata Marshall, sp. nov.

(Figures 29, 31, 34, 37)

Description: Shell (holotype) 3.35 mm high, slightly higher than broad, spire evenly conical, 1.05 \times height of aperture, anomphalous, thin, translucent, glossy, nacreous through thin outer shell layer. Purplish brown beside suture on protoconch and first 0.25 teleoconch whorl. Subsequent whorls with median and peripheral bands of opaque white that are regularly interrupted by V-shaped, spirally dislocated axial bands of yellowish brown, axial bands extending as irregular zigzags across base. Columella opaque white.

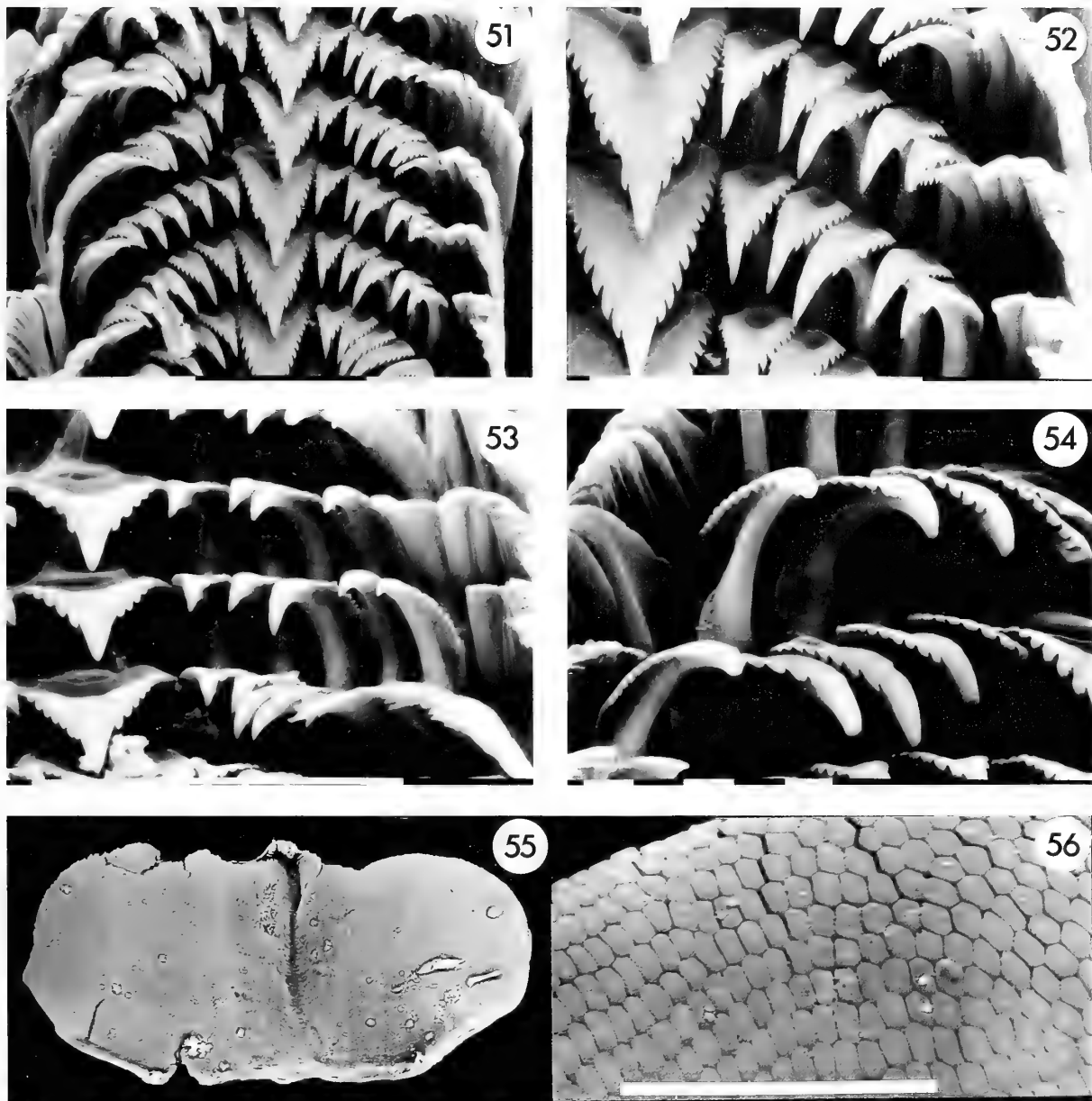
Protoconch 320 μ m wide, sculptured with few fine, crisp spiral threads.

Teleoconch of 4.25 convex whorls, periphery subangulate, base gently rounded. First 1.75 whorls with 4 fine, crisp spiral threads on abapical half, abapical spiral bordering suture and persisting throughout, others progressively weakening and vanishing, the last vanishing at end of 2nd whorl. Three fine spiral threads on outside of columella. Columella thick, vertical. Aperture subcircular. Outer lip thin, inner lip thick, parietal glaze thin. Collabral growth lines prosocline on spire, sigmoidal on base.

Animal unknown.

Type data: Holotype MNZ M.247716 (3.35 \times 2.75 mm, 4.25 teleoconch whorls) and juvenile paratype MNZ: BS 884 (0.630), 32°32.6'S, 167°29.2'E, summit of Wanganella Bank, Norfolk Ridge, dead, 133 m, r.v. *Tangaroa*.

Distribution: Wanganella Bank, southern Norfolk Ridge, 133 m (dead).



Explanation of Figures 51 to 56

Figures 51–54. *Kaiparathina daedala* Marshall, sp. nov., holotype radula. Figure 51. Entire width. Figures 52–54. Details of central and lateral teeth.

Figures 55, 56. *Kaiparathina coriolis* Marshall, sp. nov., holotype jaw, ventral (interior) surface, anterior edge at top. Figure 55. Jaw width 1.60 mm. Figure 56. Detail of jaw elements of anterior edge. Scale Figures 51, 52, 53, 56 = 100 µm, Figure 54 = 25 µm.

Remarks: *Kaiparathina fasciata* differs from the holotype of *K. navakaensis* by being much thinner-shelled, by having a more exert protoconch and slightly, but distinctly, more strongly convex whorls, and by color pattern. It differs from *K. boucheti* by having a substantially smaller protoconch (width 320 µm instead of 400–420 µm), by being more weakly and sparsely sculptured, and by having a

color pattern on the teleoconch. It differs from *K. prae-cellens* by being thinner-shelled, more narrowly conical, and smaller in size relative to the number of whorls. *Kaiparathina fasciata* is substantially smaller than *K. coriolis*, which also differs in details of sculpture, color and color pattern.

Etymology: Banded (Latin).

Kaiparathina daedala Marshall, sp. nov.

(Figures 30, 32, 33, 35, 36, 38, 40, 41, 51–54)

Description: Shell up to 4.65 mm high, usually higher than broad, spire 0.9–1.2× as high as aperture, anomphalous, of moderate thickness, glossy, nacreous within. Protoconch tip purplish brown. Teleoconch color variable. Holotype: first 2 whorls translucent white, subsequent spire whorls and base pinkish buff with narrow supra- and subsutural bands; suprasutural band (on peripheral keel) of reddish brown spots, subsutural band white; scattered reddish brown spots on base. Paratype with supra- median and suprasutural (on peripheral keel) rows of pinkish gray spots, ground color predominantly white over adapical half of whorl and pale pinkish gray below and on base, the latter mottled in paler and darker shades. Inner lip white, rim darkly pigmented.

Protoconch 370 μ m wide, sculptured with 3 fine, crisp spiral threads, otherwise smooth.

Teleoconch of up to 4.7 convex whorls; periphery becoming rounded on last adult whorl, broadly angulate before; base weakly convex. First 2 spire whorls sculptured with 4 rounded spiral threads that may multiply by intercalation to number 6, adapical margins sharply defined; abapical spiral becoming strongest, persisting as peripheral keel, adapical margin exposed on spire; other spirals weakening late on 2nd whorl and vanishing early on 3rd whorl, spiral bordering peripheral spiral sometimes (paratype) persisting throughout. Subsequent whorls smooth apart from obscure spiral lines, and collabral growth lines; in paratype, however, 13 similar, rounded spiral threads resolve on last half of last adult whorl. Base with 14–16 rounded spiral threads, most of those on outer third resolving on last half of last adult whorl. Collabral growth lines shallowly sigmoidal on spire, more deeply sigmoidal on base. Aperture subquadrate; outer lip thin at rim, thicker and simple within; inner lip thick, parietal glaze very thin.

Animal (reconstituted): operculum and jaws similar to those of *Kaiparathina boucheti* and *K. coriolis*.

Radula (Figures 51–54). Central tooth similar to that in *Kaiparathina coriolis*, lateral (5 pairs) and marginal teeth similar to those in *K. vaubani*.

Type data: Holotype MNHN (4.65 \times 3.80 mm, 4.70 teleoconch whorls), *Marion-Dufresne* cruise 32 sta. CP57, 21°05'S, 55°11'E, off Réunion, alive, 210–227 m. Paratype MNHN (4.05 \times 3.80 mm, 4.30 teleoconch whorls), *Marion-Dufresne* cruise 32 sta. DC 128, 20°51'S, 55°36'E, off Réunion, dead, 280–340 m.

Distribution: Off Réunion, 210–340 m, living at 210–227 m.

Remarks: *Kaiparathina daedala* is distinctive in having numerous spiral threads on the base. The terminal cusp of the central tooth is small as in *K. coriolis* instead of stiletto-like as in *K. boucheti* and *K. vaubani*.

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NOTES, INFORMATION & NEWS

Prey Attack by the Patagonian Octopus *Octopus tehuelchus* d'Orbigny: an Odd Pattern

by

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Introduction

Most octopus species are opportunistic (MANGOLD, 1983; AMBROSE, 1984) and versatile predators that use different techniques to overcome their prey: (1) some crab prey are killed with a toxin (NIXON & BOYLE, 1982); (2) hermit crabs can be either pulled from their shells (FAWCET, 1984; BROOKS & MARISCAL, 1985) or their shells can be drilled (WODINSKY, 1969); and (3) shelled mollusks are usually drilled, although some are killed by pulling apart their valves (FUJITA, 1916; PILSON & TAYLOR, 1961; ARNOLD & ARNOLD, 1969; HARTWICK *et al.*, 1978).

Octopus tehuelchus d'Orbigny, a small-sized species distributed along the southwestern Atlantic (CARCELLES, 1940; CASTELLANOS & MENNI, 1969), reaches high densities in the intertidal and shallow subtidal zones (up to 15 m depth) of the San Matias Gulf, Argentina (41°S; IRIBARNE, 1990). In contrast with other octopus species, it is not a generalist predator (IRIBARNE *et al.*, 1991). Either the hard shells or chemical defenses of prey appear to be the main octopus deterrents (IRIBARNE *et al.*, 1991).

In this note we report that the Patagonian octopus overcomes hermit crabs (*Pagurus* sp.) by drilling the gastropod (*Tegula patagonica* d'Orbigny) valves used as shelter but never drills the shell when attacking the living gastropod (*T. patagonica*) itself. Implications of this pattern of attack are discussed.

Materials and Methods

This study was conducted under laboratory conditions with octopuses and prey species collected in the San Antonio Bay, northern Patagonia, Argentina (41°S, 63°30'W). *Octopus tehuelchus*, the gastropod *Tegula patagonica*, and the hermit crab *Pagurus* sp. are commonly found in the study area. Shells of *T. patagonica* are the most common shelter used by hermit crabs *Pagurus* sp. in this area (personal

observations, Iribarne and Fernandez) and both are prey of the Patagonian octopus (personal observations, Iribarne and Fernandez). Octopus and potential prey species were collected by diving, taken to the laboratory, and held in 60-L seawater tanks with temperature and salinity close to field conditions. The water was exchanged every other day to eliminate nitrogenous wastes. Brooding females were discarded due to low feeding activity (POLLERO & IRIBARNE, 1988). Before each trial octopuses were starved for 24 hr and weighed. Shells of living gastropods were measured (total height) and hermit crab shelters were measured (total height) and scrutinized for evidence of octopus drilling to avoid using already drilled hermit crab shelters. Independent experiments were conducted with each prey species. Octopuses (17 to 56 g) were offered two individuals of *T. patagonica*, equally distributed between two size classes (<10 mm and >10 mm height; replicated 10 times) or with two individuals of hermit crabs *Pagurus* sp. living in *T. patagonica* shell, one of each size class (<10 mm and >10 mm height; replicated 12 times). After 24 hr prey remains were carefully scrutinized with a binocular microscope for evidence of drilling. When holes were present the major axis (diameter) of the external border of the bored hole was measured to 0.01 mm.

Results and Discussion

Twenty percent of the *Tegula patagonica* offered were consumed but none of them drilled. Fifty-five percent of the hermit crabs sheltering in the *T. patagonica* were consumed and all the gastropod shells were drilled. Most holes were found in the second whorl of the shell, but some were located in the spire closer to the last whorl or in the last whorl. In 20% of the cases octopuses made two holes in different whorls, both perforating the shell. It is unknown which hole was bored first. The outer diameter of the holes ranged from 0.35 to 0.59 mm ($\bar{x} = 0.46$, $SD = 0.087$, $n = 13$) and was not correlated with octopus weight ($r = 0.55$, $df = 11$) or shelter size ($r = 0.2$, $df = 11$). The diameter of the hole decreased from the external border towards the internal cavity as occurs with *O. vulgaris* Cuvier drilling *Mytilus edulis* Linnaeus (NIXON, 1979), *Pitaria chione* Linnaeus, and *Venus verrucosa* Linnaeus (AMBROSE & NELSON, 1983). Drilling on hermit crabs has been previously reported by WODINSKY (1969). Hermit crabs reduce predation by a variety of behavioral means, the simplest one being retraction into the shell (KOBAYASHI, 1986). The relatively high number of double complete holes may indicate a high rate of failure in the attacks.

Octopus predation on mollusks has been inferred from prey remains based on the presence of bore holes (ROBBA & OSTINELLI, 1975; STANTON & NELSON, 1980; FAWCET,

1984; EVANS, 1980–1981; VERMEIJ, 1987). Our results show that hermit crabs are preyed upon by drilling shells of *Tegula patagonica*, which interestingly were never drilled when the gastropod was the prey. This result contrasts with those found for *Octopus* sp. and *Tegula funebris* Adams along the northeastern Pacific coast, where the gastropod is always drilled, but drilling is unlikely when *T. funebris* shells are inhabited by hermit crabs (FAWCET, 1979). These different outcomes suggest that caution should be exercised when octopus predation on gastropods is inferred from prey remains.

Acknowledgments

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Examples of Damage Repair in the Shell of the Cephalopod Genus *Argonauta*

by

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ARNOLD (1985) reported on damage and subsequent repair in the shell of the cephalopod *Nautilus pompilius* Linnaeus, 1758. This study was important in understanding the life history of *Nautilus*, specifically, predation on it. The cephalopod genus *Argonauta* comprises a group of octopods that utilize a thin unichambered exoshell, which functions as an egg case and is carried for only a short duration compared to the lifetime shell of *Nautilus*. While not having the significance of the phenomenon in the *Nautilus* shell, breakage and repair do occur in the *Argonauta* shell. Examples of damage and repair in the *Argonauta* shell are briefly discussed here.

There are two types of abnormal growth in *Argonauta* shells. One of these abnormalities is nonsymmetrical growth of the shell. The shell is created by secretions from two lobes on the number one arm pair of the female animal. Irregular secretion rates of the lobes result in nonsymmetrical shells (Figure 1A). The common results of nonsymmetrical growth in *Argonauta* shells are uneven tubercle lengths of the two keels on the back of the shell and different structures of the two tips of the aperture (Figure

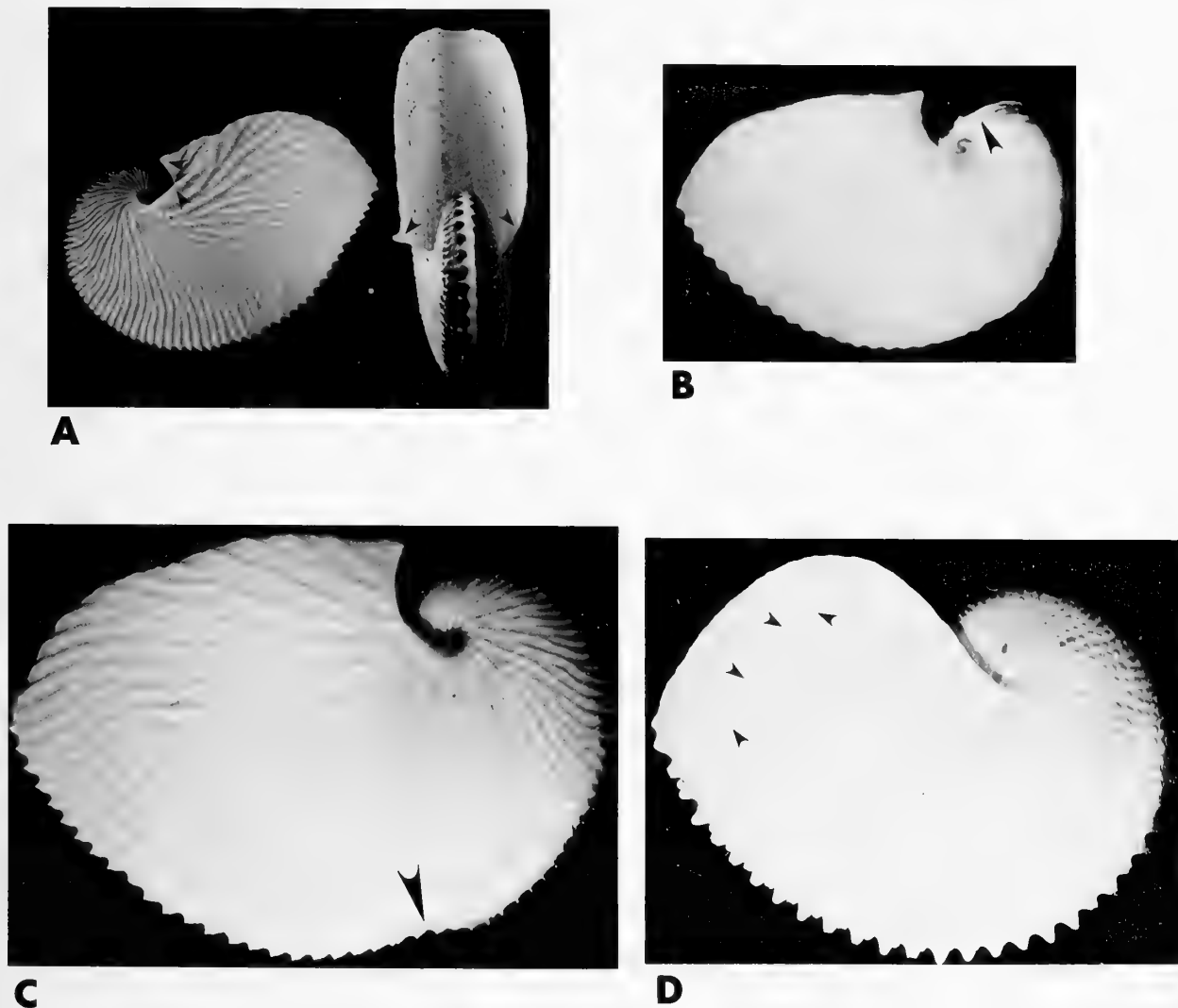


Figure 1

A. Examples of nonsymmetrical *Argonauta* shells showing different structures of the tips of the aperture at the umbilical region of the shell. At left is a side view of a specimen of *A. argo* (225 mm) and at right is an apertural view of a specimen of *A. nodosa* (210 mm). The tips of the aperture at the umbilical region of the shells are indicated by arrows. B. A specimen of *A. argo* (115 mm) with shell repair at the early whorl of the shell, resulting in an abnormal flattening of the early whorl structure. The repaired area of the shell is indicated by the arrow. C. A specimen of *A. argo* (145 mm) with shell repair on the keel region of the shell, resulting in a depression on the backside of the shell. The depression area of the shell is indicated by the arrow. D. A specimen of *A. nodosa* (216 mm) with damage and continual shell secretion at the aperture area of the shell. The growth scar is indicated by arrows.

1A) where the aperture meets the umbilical region of the shell.

The second type of abnormal growth on *Argonauta* shells results from shell damage and repair by the female. Severe shell damage can result in patching of the shell, which does not include resumption of the shell pattern. The patching may result in the reattachment of broken shell fragments. An example of such shell damage is shown in Figure 1B, where a shell of the species *Argonauta argo*

Linnaeus, 1758, has been repaired in the early whorl of the shell. The shell patch is flat and the normal curving structure of the early whorl is not recreated. Less traumatic shell breakage and repair will result in the resecretion of the shell's normal pattern. Examples of this less traumatic shell damage and repair are shown in Figure 1C, D. In Figure 1C, damage to the keel area of a specimen of *A. argo* has resulted in a depression in the backside of the shell. A specimen of *Argonauta nodosa* Lightfoot, 1786, is

shown in Figure 1D. This shell has experienced damage and continual secretion of the shell at the aperture area of the shell.

ARNOLD (1985) concluded that massive mechanical shell damage to the shell of *Nautilus pompilius* could be rectified by the animal. It appears that similar damage to the shell of the female *Argonauta* can also be successfully corrected by the animal. The cause of shell damage in *Nautilus* is

largely predation (ARNOLD, 1985) and I assume that predation is also largely responsible for the shell damage in *Argonauta*.

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Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, not justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

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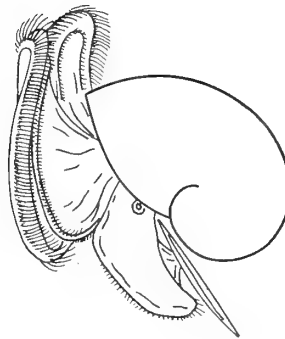
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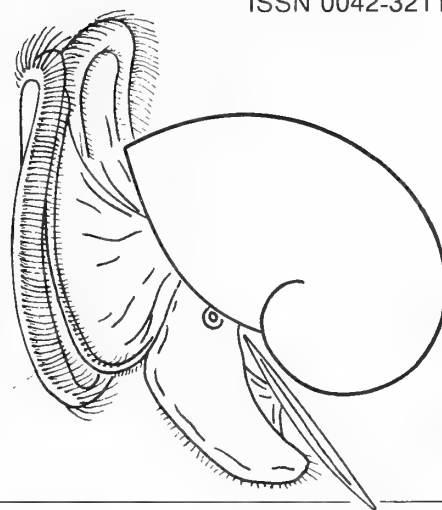
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THE VELIGER

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Energetic Implications of Variation in Pedal Mucus Production by *Patella vulgata* Linnaeus, 1758

by

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Abstract. The important role played by pedal mucus production in the flow of energy within intertidal mollusks has been recognized. However, thus far, intraspecific variation in mucus production has not been considered. This study demonstrates that mucus production varies both spatially and temporally. Mucus production rates by immersed limpets, *Patella vulgata* Linnaeus, 1758, from one population showed temporal variation of up to about five-fold. A population of high-shore limpets produced mucus at about twice the rate of mid- and low-shore populations. Limpets on a semi-exposed shore produced mucus at about 1.5 times the rate of those on a moderately sheltered shore. These differences may be due to spatial differences in activity. When stationary, limpets secrete adhesive mucus only within the first 10 min of attachment and mucus production is proportional, as expected, to animal weight^{3/4}. Spatial and temporal differences between conspecific populations in terms of an energetically important process (mucus production) will produce differences in energy balance. The results are discussed in terms of the important consequences of variation in physiological processes to the description of energy flow and the concept of the “energy budget.”

INTRODUCTION

Carefully compiled descriptions of energy flow or “energy budgets” can help to produce an understanding of energy transfer through ecosystems. Such studies focused on intertidal grazers (see HAWKINS & HARTNOLL, 1983, for review) can show the importance of these species in terms of energy flow within the littoral community. Recently, however, it has been realized that many such studies involving marine mollusks, particularly gastropods, are incomplete. Numerous works (EDWARDS & WELSH, 1982; HORN, 1986; PECK *et al.*, 1987; DAVIES *et al.*, 1990a) have discovered that mucus, which was hitherto ignored, can play an important role in the energetics of these species, comprising up to 70% of consumed energy (HORN, 1986). However, in each case mucus was measured under one set of conditions only and no attempt was made to discover any variation in its production or the factors which may be responsible for this.

In gastropods most mucus is produced for use in locomotion where, in *Littorina littorea*, DAVIES *et al.* (1992a) showed its cost in energy terms to be over 35 times that

of the metabolic cost of locomotion. Although mollusks might be expected to produce mucus at a functionally minimal level, it must be recognized that mucus may have functions other than locomotion (*e.g.*, as a protective barrier, or in trail following, see DENNY, 1989). Because the roles these functions play in molluscan biology are likely to vary with environmental factors (including pollution, DAVIES, 1992), the same rates of mucus production might not be expected to be shown by different populations. This is particularly likely when locomotory activity differs between populations (see LITTLE, 1989).

This paper aims to demonstrate that caution should be exercised in interpreting the results from ecophysiological studies, such as those on mucus production, owing to the labile nature of physiological processes themselves. Despite its historical omission from energy budgets, the simple insertion of a “mucus” term into a budget could be erroneous unless the variability of mucus production with environmental factors has been assessed. Using the limpet *Patella vulgata* Linnaeus, 1758, as an example organism, I aimed to investigate how the production of an energetically expensive product, mucus, can vary intraspecifically both spatially and temporally, and what might cause that variation. Results are reported of experiments assessing variation in immersed mucus production from one popu-

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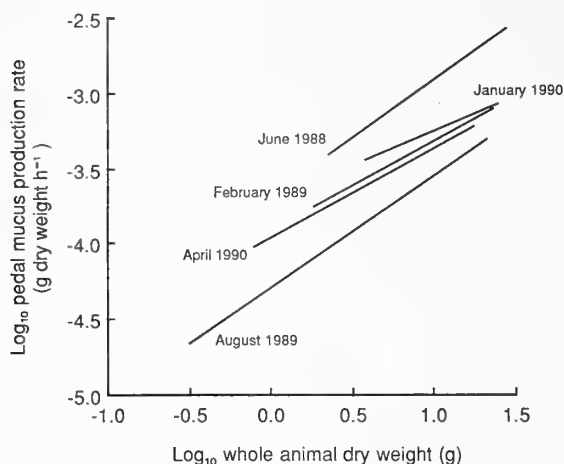


Figure 1

Temporal variation in pedal mucus production rates by *Patella vulgata* immersed in seawater. Regression data given in Table 1.

lation over time and variation between populations whose habitats differ in shore height and wave exposure. In addition, since many populations of *P. vulgata* spend a large proportion of their time inactive (see HARTNOLL & WRIGHT, 1977; LITTLE, 1989), the timing of mucus production during this stationary phase was investigated by recording pedal mucus secretion after increasing periods of attachment. When limpets are stationary, the amount of mucus they produce may be a function of pedal area, since the pedal sole is the site of secretion of the adhesive mucus (GRENON & WALKER, 1978). Thus stationary mucus production should be a function of animal weight^{2/3} since foot area grows in isometric proportion to weight (unpublished data). This can be tested using my experimental data.

MATERIALS AND METHODS

When collecting *Patella vulgata*, both the animal and the rock on which it was situated were removed and taken to the laboratory. Limpets were then easily lifted from the rock after they had moved away from their home scars. Experiments on limpets from the Isle of Man were performed at Port Erin, Isle of Man within 12 hr of collection.

The experimental apparatus consisted of a large glass plate in a shallow tank into which fresh seawater flowed continually. The temperature of the water was maintained at 10°C. To assess pedal mucus production by immersed limpets, the foot of each animal was gently scraped free of feces, mucus, and other debris, and the animal placed in the center of the plate. After 6 hr (the mean time of immersion or emersion by the tide at MTL) each was removed from the plate, its foot scraped clean of mucus with a single sweep of the rounded end of a pair of forceps (DAVIES *et al.*, 1990a), and the mucus added to that adhering to the plate. A razor blade was used to scrape the plate free of mucus and the mucus was dried at 70°C and weighed to 0.1 mg. The dry weights of limpet shell and flesh were separately determined and summed to give whole animal dry weight.

To study the temporal range of mucus production rates exhibited by one population, pedal mucus production rates of immersed limpets were determined as above for limpets collected from MTL at Derbyhaven, Isle of Man (Grid Reference SC 294 685) in June 1988, February 1989, August 1989, January 1990, and April 1990. The shore is moderately sheltered and rates about five on BALLANTINE's (1961) scale of exposure. This scale grades shores from "one" (extremely exposed) to "eight" (extremely sheltered) depending on the biota present. Sample sizes ranged from 10 to 50 animals.

The effect of shore height was examined by determining pedal mucus production rates for 20 animals collected each from horizontal surfaces at high-shore, MTL, and low-shore at Derbyhaven in February 1989. The effect of wave exposure on mucus production was assessed using samples of 20 *Patella vulgata* collected in February 1989 from horizontal surfaces at mid-shore at both Port St. Mary, Isle of Man (Grid Reference SC 208 669), a semi-exposed shore which rates about four on BALLANTINE's (1961) scale, and St. Michael's Island, Isle of Man (Grid Reference SC 294 674), a very sheltered shore which rates about seven.

Limpets used to determine when during the 6-hr (at MTL) stationary period the adhesive pedal mucus is secreted were collected from MTL at Rhosneigr, Anglesey, Wales (Grid Reference SH 314 729) in November 1989. They were transported to the laboratory at Man-

Table 1

Calculated relationships between pedal mucus production rate (y , g dry weight hr^{-1}) and whole animal dry weight (x , g) for *Patella vulgata* immersed in seawater. Temporal variation. Ranges given are SE.

	Equation	n	r^2	P
June 1988	$y = 2.214 \times 10^{-4} \pm 2.30 \times 10^{-5} \cdot x^{0.766 \pm 0.014}$	50	0.569	<0.001
February 1989	$y = 1.072 \times 10^{-4} \pm 5.1 \times 10^{-6} \cdot x^{0.594 \pm 0.031}$	20	0.503	<0.001
August 1989	$y = 5.01 \times 10^{-5} \pm 2.3 \times 10^{-6} \cdot x^{0.741 \pm 0.021}$	20	0.767	<0.001
January 1990	$y = 1.950 \times 10^{-4} \pm 2.47 \times 10^{-5} \cdot x^{0.447 \pm 0.056}$	10	0.448	<0.05
April 1990	$y = 1.202 \times 10^{-4} \pm 6.6 \times 10^{-6} \cdot x^{0.594 \pm 0.028}$	30	0.349	<0.001

chester, maintained in an artificial tidal system (on a 6-hr immersion, 6-hr emersion cycle) and used within four days. Limpets were placed singly on small glass plates for periods of 1, 2, 3, 5, 10, 20, and 30 min and 1, 2, 4, and 6 hr in an environment of 10°C and 70% relative humidity. After the allotted time the limpets were removed and the pedal mucus produced was collected and measured as before. Sample sizes in each time period were nine or ten limpets.

RESULTS

There is wide variation (up to above five-fold) in pedal mucus production rate by immersed *Patella vulgata* from Derbyhaven depending on the date of measurement (Figure 1). The regression lines constructed for data collected in February 1989, January 1990, and April 1990 have the same elevation (intercept) (ANCOVA, $F_{2,56} = 0.9$, $P > 0.5$), but the June 1988 line shows a significantly higher elevation ($F_{3,106} = 14.9$, $P < 0.001$) and the August 1989 line a significantly lower elevation ($F_{3,76} = 4.2$, $P < 0.02$). Thus mucus production rate was greatest when assessed in June 1988 and least in August 1989, with those assessments in February 1989, January 1990, and April 1990 of intermediate value. The slopes of each regression line (Table 1) are, however, not significantly different ($F_{4,121} = 0.7$, $P > 0.1$)—i.e., the way in which mucus production scales with whole animal dry weight did not vary between sampling dates.

Immersed pedal mucus production rate varies with both wave exposure and shore height (Figure 2, Table 2). Limpets at mid-shore at Port St. Mary (semi-exposed shore) secreted mucus at about 1.5 times the rate ($F_{1,37} = 4.8$, $P < 0.05$) of those on the more sheltered shore at MTL at Derbyhaven (moderately sheltered). No significant correlation was found between mucus production rate and whole animal dry weight for the limpets from mid-shore at St. Michael's Island (very sheltered shore). At Derbyhaven, limpets high on the shore produced mucus at about twice the rate of those at MTL or those low on the shore ($F_{2,56} = 8.1$, $P < 0.002$). These latter groups of animals secreted mucus at rates which are not significantly different

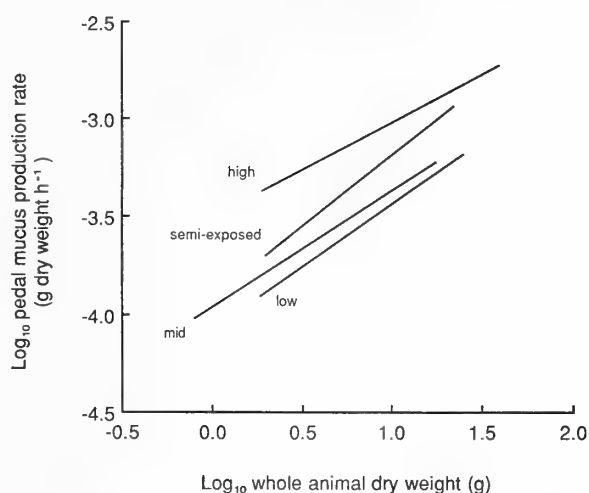


Figure 2

Pedal mucus production rates by immersed *Patella vulgata* collected from four shore positions: high-, mid-, and low-shore on moderately sheltered shore, mid-shore on semi-exposed shore. Regression data given in Table 2.

from each other ($F_{1,36} = 0.9$, $P > 0.1$). The slopes of the regression lines in Figure 2 do not differ significantly ($F_{3,71} = 0.5$, $P > 0.1$) (mean slope = 0.611) showing that the way in which mucus production scales with animal size did not vary between limpets from different areas of shore (except at St. Michael's Island).

Pedal mucus produced by emersed limpets (animals stationary) is independent of time after the first 10 min of attachment (Figure 3, Table 3). Note that Figure 3 and Table 3 express mucus in terms of weight produced and not as a rate of production. This distinction is important in actuarial bioenergetics (see RUSSELL-HUNTER & BUCKLEY, 1983). The regression lines in Figure 3 differ neither in slope ($F_{6,54} = 0.2$, $P > 0.1$) nor elevation ($F_{6,60} = 1.4$, $P > 0.1$). The mean exponent from Table 3 is not significantly different from the theoretical exponent (0.667) showing that limpet mucus production scales as expected

Table 2

Calculated relationships between pedal mucus production rate (y , g dry weight hr^{-1}) and whole animal dry weight (x , g) for immersed *Patella vulgata* collected from different shore heights at Derbyhaven (moderately sheltered shore) and from mid-shore at Port St. Mary (semi-exposed shore). Ranges given are SE.

	Equation	n	r^2	P
Derbyhaven				
high-shore	$y = 3.090 \times 10^{-4} \pm 1.72 \times 10^{-5} \cdot x^{0.485 \pm 0.022}$	20	0.578	<0.001
mid-shore	$y = 1.072 \times 10^{-4} \pm 5.1 \times 10^{-6} \cdot x^{0.594 \pm 0.031}$	20	0.503	<0.001
low-shore	$y = 8.51 \times 10^{-5} \pm 7.0 \times 10^{-6} \cdot x^{0.626 \pm 0.046}$	19	0.365	<0.001
Port St. Mary				
mid-shore	$y = 1.175 \times 10^{-4} \pm 6.4 \times 10^{-6} \cdot x^{0.738 \pm 0.028}$	20	0.664	<0.001

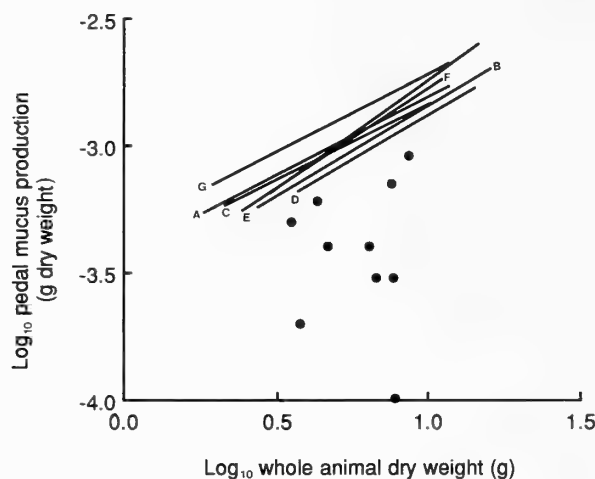


Figure 3

Pedal mucus production by *Patella vulgata* as a function of whole animal dry weight for animals left to adhere to glass in air at 70% relative humidity for time periods from 5 min to 6 hr. Data points are for 5 min of attachment. Regression lines are for other periods (A = 10 min, B = 20 min, C = 30 min, D = 1 hr, E = 2 hr, F = 4 hr, G = 6 hr). Regression data given in Table 3.

with animal weight. One, 2, and 3 min experimental periods did not result in the production of any mucus and limpets did not attach. After 5 min mucus was secreted and although there is no significant correlation between mucus production and whole animal dry weight, all the datum points (Figure 3) are below the other regression lines. Thus less mucus was produced than after 10 or more min. Only two out of the 10 experimental animals were found to be attached after 5 min, while after 10 min and longer experimental periods all the animals were firmly attached.

DISCUSSION

The results of this study must be considered with due regard to placing limpets in an artificial environment. Di-

rect extrapolation of laboratory behavior to the field is difficult and this must be borne in mind when the results are considered. Movement in the laboratory (less than ≈ 0.2 m from the center of the plate) was less than in the field observations of HARTNOLL & WRIGHT (1977) conducted at Derbyhaven (mean foraging distance = 0.4 m); and the substratum in the field is probably considerably rougher than the experimental substratum. Pedal mucus production rate by *Haliotis tuberculata* has been shown to increase with the particle size (roughness) of the substratum (CULLEY & SHERMAN, 1985). Because there was little water movement in the experimental tanks, little mucus would have been lost into the water. DAVIES *et al.* (1992b) have shown that mucus decay in seawater is primarily due to the mechanical action of the seawater.

The reasons for temporal variation in mucus production are unclear but may reflect activity differences produced by varying environmental conditions. Limpets may have moved less on the experimental plates in August than in June and the winter months. Tentatively, this could be because during late summer the gonad competes for space within the animal with the visceral mass, making locomotion difficult (ORTON *et al.*, 1956). DAVIES *et al.* (1990b) reported seasonal variation in the composition of *Patella vulgata* pedal mucus which may be related to the breeding cycle.

The increases in pedal mucus production rate up shore and with wave exposure may reflect differences in limpet activity or imply mucus is secreted onto the sole at different rates depending on shore position. Both high-shore and exposed-shore limpets may have their foraging periods restricted by limited immersion time (assuming limpets only forage when the tide is in, as is the case at Derbyhaven, HARTNOLL & WRIGHT, 1977, and personal observations). and violent wave action, respectively. Thus when immersed in experimental tanks, limpets from these environments may attempt to maximize their food intake and so are more active than limpets from lower down the shore or from less exposed shores. Adjacent populations of limpets have been shown to differ markedly in foraging behavior (LITTLE *et al.*, 1991).

Table 3

Calculated relationships between weight of pedal mucus produced (y , g dry weight) and whole animal dry weight (x , g) for *Patella vulgata* left to adhere to glass for time periods from 10 min to 6 hr. Ranges given are SE. t -value describes the goodness of fit of the calculated exponent to the theoretical exponent (0.667).

	Equation	n	r^2	P
10 min	$y = 3.715 \times 10^{-4} \pm 3.51 \times 10^{-5} \cdot x^{0.617 \pm 0.065}$	10	0.529	<0.01
20 min	$y = 2.754 \times 10^{-4} \pm 2.95 \times 10^{-5} \cdot x^{0.710 \pm 0.065}$	9	0.656	<0.01
30 min	$y = 3.631 \times 10^{-4} \pm 3.21 \times 10^{-5} \cdot x^{0.600 \pm 0.051}$	10	0.638	<0.01
1 hr	$y = 2.630 \times 10^{-4} \pm 4.50 \times 10^{-5} \cdot x^{0.694 \pm 0.088}$	9	0.498	<0.05
2 hr	$y = 2.512 \times 10^{-4} \pm 4.51 \times 10^{-5} \cdot x^{0.853 \pm 0.114}$	10	0.413	<0.05
4 hr	$y = 2.692 \times 10^{-4} \pm 3.27 \times 10^{-5} \cdot x^{0.791 \pm 0.075}$	10	0.584	<0.02
6 hr	$y = 4.677 \times 10^{-4} \pm 6.16 \times 10^{-5} \cdot x^{0.606 \pm 0.050}$	10	0.407	<0.05
mean exponent = 0.696 ± 0.027 , $t = 1.062$, $0.2 < P < 0.5$				

The reasons for the lack of correlation between mucus production and animal size only on the very sheltered shore are unclear. However, conditions on this shore are different from those on the more exposed shores. The very sheltered shore is dominated by fucoid algae, with limpets occurring singly (rather than in clumps, as on the other shores) underneath the algal canopy. The individual limpet foraging pattern on this shore could be dependent more on microhabitat than on any factor affecting the shore as a whole.

The lack of secretion of pedal mucus after the first 10 min of attachment is not surprising. Since limpets are stationary, only enough mucus to facilitate adhesion will be secreted. This implies that mucus maintains its functional capability (adhesive properties) over at least 6 hr and that there are long periods during which the pedal secretory apparatus is inactive. The secreted mucus will be important in defense against predators because of its role in adhesion (DENNY, 1980). The scaling of mucus production with animal weight^{2/3} suggests that "stationary" mucus is secreted from all areas of the sole. This contrasts with locomotory secretions which are thought to originate from the anterior groove (GRENON & WALKER, 1978). The results suggest that when assessing mucus production from stationary limpets (as may be done to obtain estimates of the energetic cost of mucus production) measurements need be taken after 10 min of attachment only and not after however long the animals are emersed *in situ*. When limpets stop moving *in situ* they may not secrete extra mucus for adhesion but use the mucus already secreted onto the pedal sole which facilitated their last movement. Thus the value of mucus production in an energy budget may be artificially increased by measuring stationary production (see DAVIES *et al.*, 1990a). However, CONNOR (1986) found trail and stationary mucus from acmaeid limpets to have different properties (perhaps related to function), so perhaps a fresh layer of mucus is secreted at the start of a stationary period.

The differential rates of mucus production reported in this study have important implications for the assessment of that component of energy flow which is mucus. A single measurement cannot embody temporal variation (see DAVIES *et al.*, 1990a) nor be extrapolated to other populations or even other species (see CALOW, 1974). The energy drain as mucus will differ between limpets from different populations and since mucus plays a large role in the physiological energetics of limpets (DAVIES *et al.*, 1990a), the energy balance of these different populations will vary considerably. Although allometric effects make direct comparisons between populations difficult, as an example of this variation a limpet of whole dry weight 10 g can be used. Assuming the calorific value of mucus measured by DAVIES *et al.* (1990a) (8.984 kJ g^{-1}) is valid for all mucus samples (but see DAVIES *et al.*, 1990b), then depending on shore position and collection date examined in this study the energetic cost of mucus production by a 10 g immersed limpet varies from 2.5 to 11.6 J hr^{-1} . In more conventional

energy budget units, this is 10.9 to $50.8 \text{ kJ year}^{-1}$, assuming the limpet spends half its time submerged (DAVIES *et al.*, 1990a). These values represent considerable proportions of the limpet energy budget: up to 21% of consumed energy for a limpet of whole dry weight 10 g (using data from DAVIES *et al.*, 1990a, and WRIGHT & HARTNOLL, 1981). This phenomenon has also been demonstrated by HORN (1986) for the ormer *Haliotis tuberculata*. Thus assessments of energy flow should be regarded as "snapshots" whose comparative usefulness is restricted. Mucus production is to a large extent dependent on locomotory activity. Thus to describe the energetics of mucus production an understanding of movement patterns is also necessary. Limpet movement is complex but has been monitored extensively (see LITTLE, 1989, and DELLA SANTINA & CHELAZZI, 1991, for reviews). Similarly, for any species where behavior differs widely and can place drains on assimilated energy, any single expression of energy allocation or flow should be viewed with caution.

This study has demonstrated the intraspecific plasticity of an energetically important physiological process, pedal mucus production. This work suggests that before conclusions are drawn and extrapolations made from ecophysiological studies both temporal and spatial variation should be considered.

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Application of a Two-Dimensional Electrophoresis Method to the Systematic Study of Notaspidea (Mollusca: Opisthobranchia)

by

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Abstract. The phylogenetic relationships of four notaspidean opisthobranchs were examined using two-dimensional electrophoresis. The protein constituents of hearts were compared among five species belonging to four genera. The phylogeny deduced from the electrophoretic data supports the hypothesis of notaspidean phylogeny based on morphological and behavioral characters. To evaluate the validity of taxonomic ranks in the classification system proposed by Willan, the similarity values between notaspideans were compared with those obtained previously by two-dimensional electrophoresis on other animal groups. There is equivalence in electrophoretic distance at the level of genus between notaspideans and other animal groups.

INTRODUCTION

The Notaspidea is an order of opisthobranch mollusks characterized by a single gill situated on the right side of the body. WILLAN (1987) has established a new classification system of Notaspidea (Table 1) based upon an examination of 57 morphological and behavioral qualitative characters. In his study he presented a cladogram derived by Hennigian methodology and a computer-generated phenogram of 11 notaspidean genera, which are fully congruent with each other. Despite this clarification at higher levels, some confusion in the taxonomy of Japanese Notaspidea remained, mainly due to synonymy at the level of species. Recently, the senior author has proposed that Japanese notaspideans be classified into 10 species belonging to seven genera (TSUBOKAWA, 1991). However, the phylogeny of these Japanese species has not been investigated.

Two-dimensional electrophoresis is a useful technique for analyzing comprehensively protein constituents of tissues and organs. Protein electrophoretic patterns are phenotypic characters at the molecular level which reflect genetic differences between species more directly than morphological characters, though all genetic changes cannot always be detected by electrophoresis (NEI & CHAKRABORTY, 1973; NEI, 1987). Similarity and genetic distance values between species can be obtained by comparing electrophoretic patterns and can be employed for constructing dendrograms (AQUADRO & AVISE, 1981). The electrophoretic method has been applied in our serial studies to investigate phylogenetic relationships of animals (MIYAZAKI *et al.*, 1987, 1988), showing the usefulness of this method for phylogenetic analysis. In the Notaspidea, phylogenetic analysis at the molecular level has never been carried out. Therefore, application of two-dimensional electrophoresis to the systematic study of Japanese notaspideans is likely to yield new information on genetic difference and to deduce their phylogeny. Furthermore, it also permits us to evaluate Willan's phylogenetic hypothesis on the basis of molecular data.

In this study, two-dimensional electrophoresis is applied

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Table 1

Classification of the order Notaspidea
according to WILLAN (1987).

Order Notaspidea Fischer, 1883
Suborder Umbraculacea Dall, 1889
Superfamily Tylodinoidea Gray, 1847
Family Tylodinidae Gray, 1847
Genus <i>Tylo dina</i> Rafinesque, 1819
Genus <i>Anidolyta</i> Willan, 1987
Family Umbraculidae Dall, 1889
Genus <i>Umbraculum</i> Schumacher, 1817
Suborder Pleurobranchacea Férussac, 1822
Superfamily Pleurobranchoidea Férussac, 1822
Family Pleurobranchidae Férussac, 1822
Subfamily Pleurobranchinae Férussac, 1822
Tribe Pleurobranchini Férussac, 1822
Genus <i>Pleurobranchus</i> Cuvier, 1805
Tribe Berthellini Burn, 1962
Genus <i>Berthella</i> Blainville, 1825
Genus <i>Bathyberthella</i> Willan, 1983
Genus <i>Pleurehdera</i> Er. Marcus & Ev. Marcus, 1970
Genus <i>Berthellina</i> Gardiner, 1936
Subfamily Pleurobranchaeinae Pilsbry, 1896
Genus <i>Pleurobranchella</i> Thiele, 1925
Genus <i>Pleurobranchaea</i> Meckel in Leue, 1813
Genus <i>Euselenops</i> Pilsbry, 1896

to the systematic study of Japanese Notaspidea. Pairwise comparisons of electrophoretic patterns are carried out among five species belonging to four different genera. Similarity and genetic distance values are used to construct phylogenetic relationships of these species and the validity of WILLAN's (1987) phylogenetic hypothesis is discussed. The similarity values between notaspideans are compared with those obtained previously on other animal groups to evaluate taxonomic ranks in Willan's classification system.

MATERIALS AND METHODS

Samples

Five species of Japanese notaspidean opisthobranchs, belonging to four different genera, were used for pairwise comparisons. Other members of the order are rare in Japanese waters, and were not available for the present study. The combination of each pair and the locality of each animal are as follows:

- (1) *Pleurobranchus semperi* (Vayssière) from Onna, Okinawa Island versus *Umbraculum sinicum* (Gmelin) from Ōshima Island, Izu Islands.
- (2) *Berthellina citrina* (Rüppell & Leuckart) from Susaki, Izu Peninsula versus *Umbraculum sinicum* from Susaki, Izu Peninsula.
- (3) *Pleurobranchaea japonica* Thiele from off Miura Pen-

insula versus *Umbraculum sinicum* from Susaki, Izu Peninsula.

- (4) *Berthellina citrina* from Susaki, Izu Peninsula versus *Pleurobranchaea japonica* from off Miura Peninsula.
- (5) *Pleurobranchus semperi* from Onna, Okinawa Island versus *Pleurobranchaea japonica* from off Miura Peninsula.
- (6) *Pleurobranchus semperi* from Onna, Okinawa Island versus *Berthellina citrina* from Susaki, Izu Peninsula and from Kenzaki, Miura Peninsula.
- (7) *Pleurobranchus semperi* from Aka-jima Island, Kerama Islands versus *Pleurobranchus hirasei* from Ryûgû-jima, Izu Peninsula.
- (8) *Umbraculum sinicum* from Susaki, Izu Peninsula versus the same species from Irô-zaki, Izu Peninsula.
- (9) *Pleurobranchus semperi* from Onna, Okinawa Island versus the same species from Aka-jima Island, Kerama Islands.

In WILLAN's (1987) classification system (Table 1), *Umbraculum* belongs to the family Umbraculidae of the suborder Umbraculacea, one of the two suborders of the order Notaspidea. *Pleurobranchus* and *Berthellina* belong to the subfamily Pleurobranchinae of the family Pleurobranchidae of the other suborder Pleurobranchacea. *Pleurobranchaea* belongs to the subfamily Pleurobranchaeinae of the family Pleurobranchidae.

Electrophoresis

Two-dimensional electrophoresis was carried out as described in HIRABAYASHI (1981), HIRABAYASHI *et al.* (1983), and OH-ISHI & HIRABAYASHI (1988).

After narcotizing the animal, organs were dissected out in seawater, chilled on ice, and rinsed in filtered seawater to remove the blood. Then they were stored frozen at -80°C until use. Organs were homogenized with a Dounce homogenizer in 20 volumes of an extraction medium, which contained 8 M guanidine-HCl, 10% β -mercaptoethanol, and 0.1 M Tris-HCl at pH 7.5. The homogenate was dialyzed for 3.5 hr against three changes of 5 M urea, 1 M thiourea, and 0.16% β -mercaptoethanol at 0°C , and centrifuged at 40,000 rpm for 20 min with a Beckman TLA-100.3 rotor. The supernatant (40–100 μL) was subjected to first dimension isoelectric focusing with 1% agarose gel for 14,000 V·hr at 4°C . After isoelectric focusing, proteins in the agarose gel were fixed in a solution consisting of 10% trichloroacetic acid and 5% sulfosalicylic acid. The second dimension SDS-polyacrylamide gel electrophoresis, with a concentration gradient of acrylamide (12–20%), was carried out fundamentally according to LAEMMLI (1970). The proteins were stained with Coomassie brilliant blue (STEPHANO *et al.*, 1986).

Preliminary electrophoresis was conducted on several organs of *Pleurobranchaea japonica* such as heart, foot musculature, and esophagus to determine the total number of protein spots in each electrophoretic pattern. The heart

Table 2

Similarity and genetic distance among Japanese notaspideans. Similarity (F) and genetic distance (D) were calculated according to AQUADRO & AVISE (1981). Similarity, $F = 2N_{xy}/(N_x + N_y)$; Genetic distance, $D = 1 - F$. N_{xy} is the number of spots shared by members x and y in each pair, and N_x and N_y are the numbers of spots scored for x and y, respectively.

Combination	N_x N_y	N_{xy}	F	D
1 <i>Pleurobranchus semperi</i> vs. <i>Umbraculum sinicum</i>	185 27	27	0.146	0.854
2 <i>Berthellina citrina</i> vs. <i>Umbraculum sinicum</i>	177 39	39	0.220	0.780
3 <i>Pleurobranchaea japonica</i> vs. <i>Umbraculum sinicum</i>	262 65	65	0.248	0.752
4 <i>Berthellina citrina</i> vs. <i>Pleurobranchaea japonica</i>	129 26	26	0.279	0.721
5 <i>Pleurobranchus semperi</i> vs. <i>Pleurobranchaea japonica</i>	182 53	53	0.291	0.709
6 <i>Pleurobranchus semperi</i> vs. <i>Berthellina citrina</i>	256 81	81	0.316	0.684
7 <i>Pleurobranchus semperi</i> vs. <i>Pleurobranchus hirasei</i>	197 124	124	0.629	0.371
8 <i>Umbraculum sinicum</i> vs. <i>Umbraculum sinicum</i>	270 262	262	0.970	0.030
9 <i>Pleurobranchus semperi</i> vs. <i>Pleurobranchus semperi</i>	184 180	180	0.978	0.022

protein had more than 100 spots that were suitable for comparison of protein constituents, and thus the heart was used in this study.

Analysis

To compare the two-dimensional electrophoretic patterns, the triplet method (MIYAZAKI *et al.*, 1987) was used. The two samples to be compared plus their mixture were focused and electrophoresed at the same time. The electrophoretic patterns were photographed and compared visually. Overlapping of protein spots from different samples were checked against the pattern of their mixture. For correct scoring of overlapping protein spots, varying volumes of supernatants were subjected to two-dimensional electrophoresis for each combination. Similarity was calculated according to the formula $F = 2N_{xy}/(N_x + N_y)$, where F is the similarity between members x and y in each pair, N_{xy} is the number of protein spots shared by x and y, and N_x and N_y are the total numbers of protein spots scored for x and y, respectively (AQUADRO & AVISE, 1981). The genetic distance (D) was given by the formula $D = 1 - F$.

The genetic distance values of interspecific combinations (1 to 6 in Table 2) were used to construct dendrograms with the unweighted pair-group method using the arithmetic average (UPGMA) (SOKAL & MICHENER, 1958)

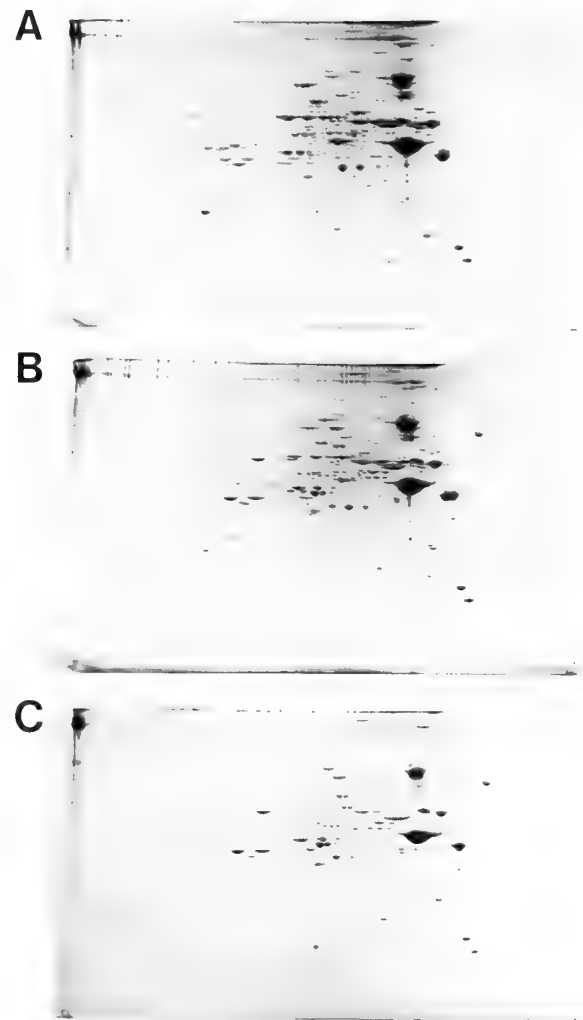


Figure 1

Typical two-dimensional electrophoretic patterns. Electrophoresis was carried out as described in the Materials and Methods section. The acidic end of the isoelectric focusing gel is to the right. The triplet method was used for comparison of protein constituents between two species. Patterns of heart proteins from *Pleurobranchus semperi* (A) and *Pleurobranchaea japonica* (C) and their mixture pattern (B) are shown here.

and modified Farris method (TATENO *et al.*, 1982) respectively. Because so few *Pleurobranchus hirasei* were obtained, this species was used only for obtaining the genetic distance of the congeneric combinations.

RESULTS

Typical two-dimensional electrophoresis patterns of hearts are shown in Figure 1. The total number of scored spots and the number of spots shared by each pair are represented in Table 2. The similarity and the genetic distance of the nine pairs are also represented in Table 2.



Figure 2

Distribution of the similarity values between Japanese notaspideans. The number corresponds with the pair number in Table 2.

Figure 2 represents a distribution of the similarity values of the nine pairs. According to WILLAN's (1987) classification system (Table 1), the values were assigned to conspecific populations (8 and 9), congeneric species (7), consubfamilial genera (6), confamilial subfamilies (4 and 5), or different suborders (1, 2, and 3). The similarity values between conspecific populations were very high (8, $F = 0.970$; 9, $F = 0.978$). On the other hand, those between consubfamilial genera (6, $F = 0.316$), confamilial subfamilies (4, $F = 0.279$; 5, $F = 0.291$), and different suborders (1, $F = 0.146$; 2, $F = 0.220$; 3, $F = 0.248$) were very low. The similarity value between congeneric species (7, $F = 0.629$) took a middle position between the above values (8–9 vs. 1–6). The order of the similarity values corresponded well with the order of the taxonomic ranks.

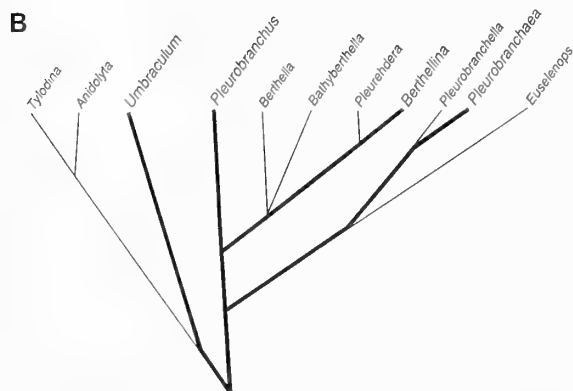
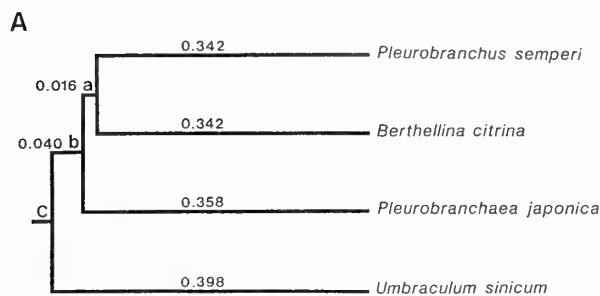


Figure 3

A. Phenogram of four notaspidean species belonging to different genera. The phenogram was constructed by UPGMA using the genetic distance values represented in Table 2. B. Cladogram of 11 notaspidean genera according to WILLAN (1987). Genera connected by heavy branches were used in this study.

The phenogram of four species belonging to different genera, *Pleurobranchus semperi*, *Berthellina citrina*, *Pleurobranchaea japonica*, and *Umbraculum sinicum*, was constructed by UPGMA (SOKAL & MICHENER, 1958) and is represented in Figure 3. The phenogram suggests that the ancestor of *U. sinicum* was the first to diverge from the common ancestor of the three other species, and next the ancestor of *Pleurobranchaea japonica* branched off from the common ancestor of the remaining two species. However, the two nodes of branches leading to the latter three species (Figure 3A, a and b) were situated very close to each other.

The UPGMA phenogram is based on the unverifiable assumption that evolutionary rates of organisms are uniform. Therefore, the modified Farris method (TATENO *et al.*, 1982) was used to construct the network and the rooted tree shown in Figure 4. The root was situated at the middle point of the longest branch connecting *Berthellina citrina* and *Umbraculum sinicum*. The modified Farris method does not rely on the assumption of uniformity of evolutionary rate, but the above rooting of the tree equates evolutionary rates of the lines leading to the two species. Another rooting method places the root on the branch connecting outgroup and ingroup clusters. Of the four species examined in this study, *U. sinicum* has been chosen as the outgroup, because the Umbraculacea (including the genus *Umbraculum*) have been separated consistently from other groups of Notaspidea (BURN, 1962; THOMPSON, 1976) because of their unique characters, including an external shell, two pairs of tentacles on an oral veil, the gill originating from the left anterolateral portion of the body, a ring-shaped thin jaw membrane in the buccal mass, and a unique internal and external reproductive system (WILLAN, 1987; TSUBOKAWA, 1991). When *U. sinicum* was treated as an outgroup, the tree was rooted between *U. sinicum* and node b, which connects the line leading to *Pleurobranchus semperi* and *B. citrina* and the line to *Pleurobranchaea japonica*. The tree is substantially consistent with the midpoint-rooted tree. The rooted tree (Figure 4B) also gave the same topology as that of the UPGMA tree (Figure 3A), though there were slight differences in branch length.

DISCUSSION

AQUADRO & AVISE (1981) have shown that genetic distance ranks obtained by two-dimensional electrophoresis are highly concordant with taxonomic levels in rodent species.

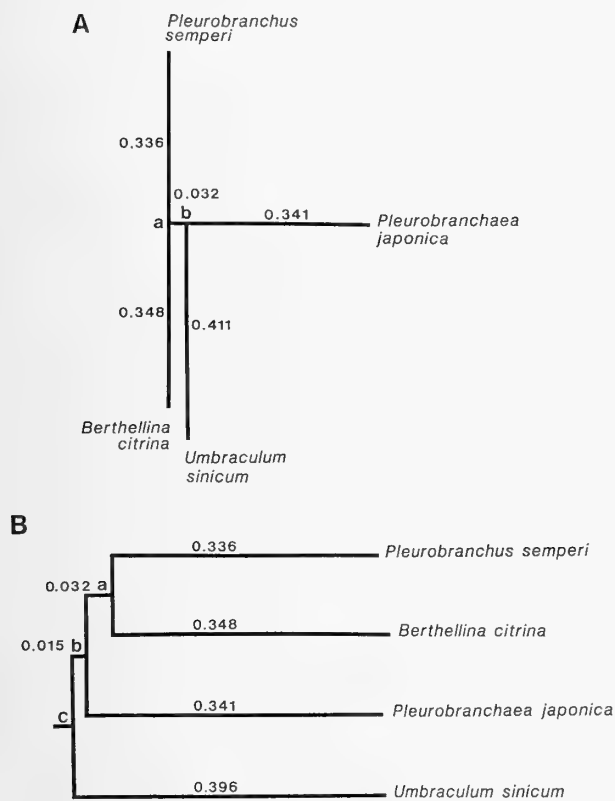


Figure 4

Unrooted network and rooted tree of four notaspidean species. The network (A) and tree (B) were constructed by the modified Farris method using the genetic distance values. The rooted tree was constructed by situating a root at the middle point of the longest branch of the network.

Furthermore, MIYAZAKI *et al.* (1987) have suggested that two-dimensional electrophoresis provides a valuable tool for systematics in estimating and evaluating genetic distances. As shown in Table 2 and Figure 2, the order of the similarity values of nine pairs corresponded with that of the taxonomic ranks based on WILLAN's (1987) classification system (Table 1). Therefore, the present results show that two-dimensional electrophoresis is a useful technique for examining phylogenetic relationships of Notaspidea, confirming the conclusions of previous studies.

When the similarity values for the Notaspidea are compared with those obtained by two-dimensional electrophoresis on animals of other groups (AQUADRO & AVISE, 1981; MIYAZAKI *et al.*, 1987, 1988), the values in the corresponding taxonomic combinations were similar between notaspideans and other animal groups (Table 3). Therefore, taxonomic ranks in WILLAN's (1987) classification system are supported by electrophoretic data. However, the values between notaspidean confamilial genera (4, 5, and 6 in Table 2) and conordinal families (1, 2, and 3 in Table 2) were low, when compared with those of rodents. A possible explanation for such differences is that ranks in rodents

Table 3

Comparison of the similarity values among four different animal groups. The similarity values are arranged in the corresponding taxonomic combinations.

Taxonomic combination	Rodent liver (AQUADRO & AVISE, 1981)	Horse-shoe crab cardiac muscle (MIYAZAKI <i>et al.</i> , 1987)	Land snail whole body (MIYAZAKI <i>et al.</i> , 1988)	Notaspidea heart (this study)
Conspecific population	0.951 0.916		0.989 0.913	0.978 0.970
Congeneric species	0.852 0.812	0.649 0.639 0.639	0.878 0.846 0.834 0.833 0.824	0.795 0.768 0.766 0.736 0.667
Confamilial genus	0.599 0.547	0.371 0.320 0.309		0.316 0.291 0.279
Conordinal family	0.504			0.248 0.220 0.146

and notaspideans are not equal. This indicates that divergence time between these notaspidean species is longer than that between rodent species in the corresponding taxonomic combination above subfamily, although the same taxonomic rank should ideally reflect the same evolutionary time in all phylogenetic lines. To formulate such an ideal and authentic classification system throughout the biological world, it is necessary to know absolute evolutionary time or relative evolutionary time. Practically, genetic distance data at the molecular level are available, because they reflect relative evolutionary time. Therefore, more comprehensive studies using several other methods are required to give accurate genetic distance measures. In the latter case, although there is no evidence which supports differences in evolutionary rates of proteins between notaspideans and rodents, the possibility cannot be excluded.

Two trees of four notaspidean genera (Figure 3A, 4B), which were depicted using the UPGMA and the modified Farris method with the present genetic distance data, gave the same topology. The topology is consistent with that of WILLAN's (1987) cladogram (Figure 3B), which was constructed on morphological and behavioral characters using Hennigian methodology. Agreement among the three trees strongly suggests reliability of the phylogenetic relationships of the four genera. However, only small differences were found in the similarity values of pairs 1 to 6 (Table 2), making the positions of three nodes (Figures 3A and 4B, a, b, and c) of the trees very close to each other. This may be ascribed to two causes. One is the high sensitivity

of two-dimensional electrophoresis for detecting differences in protein constituents. Therefore, protein differences between notaspideans, which can be detected by this method, approach a saturation level. The second is the separation of the ancestral taxa at almost the same time geologically. In either case, we must be careful to conclude that the phylogenetic relationships of the four genera are definitive, because differences in the similarity values were small, taking account of probable deviations of evolutionary changes at the molecular level. Therefore, further accumulation of phylogenetic information obtained by using other approaches is required to test the existing notaspidean phylogenetic hypothesis.

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Karyotype and Nucleolus Organizer Regions in *Ostrea puelchana* (Bivalvia: Ostreidae)

by

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Abstract. The chromosomes of the Argentinian oyster, *Ostrea puelchana*, were studied using karyometric analysis after conventional Giemsa staining, and silver-staining. The karyotype consists of 4 metacentric, five submetacentric, and one small telocentric chromosome pairs. The silver-stained nucleolus organizer regions (NORs) were terminally located on the short arms of the submetacentric pairs 2 and 4. A variable number of one to three Ag-NOR chromosomes were found within and between animals, revealing a heteromorphism in the number of active NOR sites per cell. The most frequent case was one Ag-NOR chromosome in pairs 2 and 4 simultaneously. Comparative analysis of the karyotypes of *O. puelchana*, *O. edulis*, and *O. denselamellosa* supports the taxonomic subdivision of the genus *Ostrea* into two subgenera.

INTRODUCTION

Chromosomes of Ostreacea have been studied in 24 species of four genera in Ostreidae and two genera of Pycnodontidae (see VITTURI *et al.*, 1985, and IEYAMA, 1990, for literature). Many oysters have the same chromosome number, $2n = 20$, and their karyotypes consist of only metacentric and submetacentric chromosomes. But as investigated species increase, different chromosome numbers ($2n = 18$) have been observed (IEYAMA, 1990) as well as karyotypes with subtelocentric or telocentric chromosomes (THIRIOT-QUIÉVREUX, 1984; VITTURI *et al.*, 1985; IEYAMA, 1990). Interspecific chromosomal differences in Ostreacea consist mainly of different proportions of morphological chromosome types. But studies of the nucleolus organizer regions (NORs) have also shown interspecific differences (THIRIOT-QUIÉVREUX & INSUA, 1992).

According to HARRY (1985), the genus *Ostrea* Linné, 1758, includes two subgenera, *Ostrea s.s.*, which includes *Ostrea (Ostrea) edulis* Linné, 1758, and *Ostrea (Ostrea) denselamellosa* Lischke, 1869, and *Eostrea* Ihering, 1907, with *Ostrea (Eostrea) puelchana* D'Orbigny, 1841.

Karyotypes and NORs were previously studied in *Ostrea edulis* (THIRIOT-QUIÉVREUX, 1984; THIRIOT-QUIÉVREUX & INSUA, 1992) and in *O. denselamellosa* (INSUA & THIRIOT-QUIÉVREUX, 1991). These two species are karyologically

distinguished by different proportions of metacentric chromosomes and by the different locations of the NORs in the karyotypes.

In the present paper, the karyotype and NORs were studied in *Ostrea (Eostrea) puelchana* in order to analyze cytotaxonomical relationships within the genus *Ostrea*.

MATERIAL AND METHODS

Specimens came from the experimental rearing of Argentinian *Ostrea puelchana* carried out in IFREMER French oyster farming site.

Oysters from 3 to 4 cm were incubated for 8 hr with 0.005% colchicine in seawater. The gills were then dissected and treated for 30 min in 0.9% sodium citrate in distilled water. The material was then fixed in a freshly prepared solution of absolute alcohol and acetic acid (3:1) with three changes of 20 min duration. Each slide preparation was made from one individual oyster using an air-drying technique (THIRIOT-QUIÉVREUX & AYRAUD, 1982). For conventional karyotypes, slides were stained directly with Giemsa (4%, pH 6.8) for 10 min. Photographs of suitable mitotic metaphases were taken with a Zeiss III photomicroscope, and after karyotyping, chromosome measurements of 10 cells in mitotic metaphase were made with a digitizer (Summa Sketch II) interfaced with a Macintosh Classic. Data analysis was performed with the Excel macro program. Terminology relating to centromere position follows that of LEVAN *et al.* (1964).

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Table 1
Chromosome measurements and classification derived from 10 metaphase cells of *Ostrea puelchana*.

Chromosome pair no.	Relative length		Arm ratio		Centromeric index		Classifi- cation
	Mean	SD	Mean	SD	Mean	SD	
1	13.957	0.702	0.818	0.047	44.776	1.428	m
2	12.287	0.803	0.548	0.043	35.196	1.754	sm
3	11.610	0.551	0.832	0.093	45.223	2.537	m
4	11.135	0.602	0.478	0.044	32.171	1.969	sm
5	10.339	0.409	0.474	0.055	31.889	2.461	sm
6	10.012	0.274	0.775	0.071	43.487	2.256	m
7	9.081	0.650	0.358	0.031	26.157	1.615	sm
8	8.274	0.643	0.805	0.071	44.442	2.134	m
9	8.111	0.371	0.521	0.068	34.000	3.085	sm
10	5.194	0.361	0.058	0.015	5.387	1.354	t

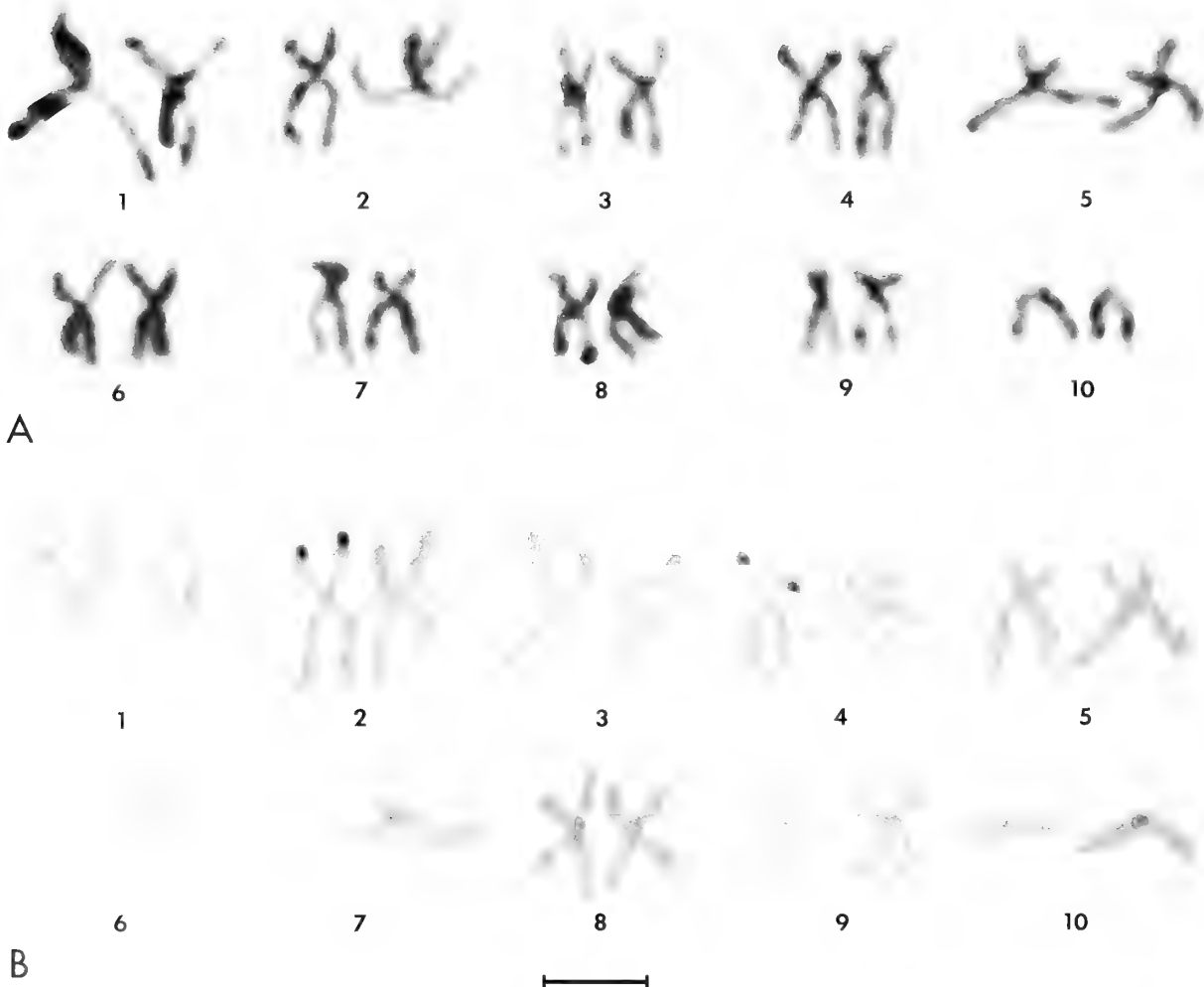


Figure 1
Karyotypes of *Ostrea puelchana*. A. Conventional Giemsa staining. B. Silver-staining. Note one chromosome with Ag-NORs in chromosome pairs 2 and 4.

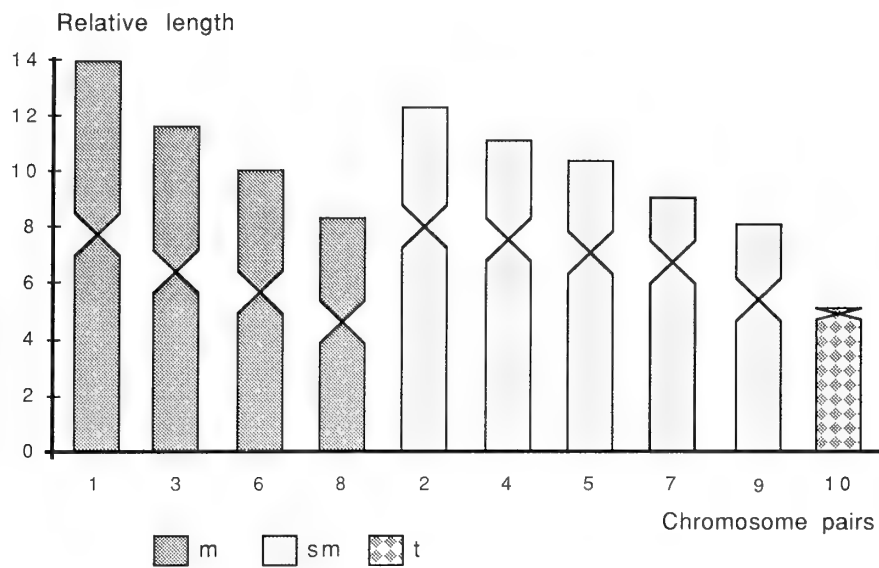


Figure 2

Ideogram constructed from relative length and centromeric index values in *Ostrea puelchana*.

The NORs were silver-stained either directly on unstained slides using the technique of HOWELL & BLACK (1980), modified by GOLD & ELLISON (1982), or on Giemsa-stained slides followed by destaining with alcohol.

RESULTS

A diploid complement of $2n = 20$ was found in 70 mitotic metaphases from 13 animals. Nine animals were randomly selected and a total of 263 metaphases were scored for chromosome counts. The percentage of aneuploid cells ($2n = 17, 18, \text{ or } 19$) was 10.65%.

For karyotyping, the chromosomes of 22 well-spread metaphase plates were cut out from photomicrographs and paired on the basis of size and centromere position. Chro-

sosome measurements were taken from the 10 best spreads and the means and SD of relative length ($100 \times \text{absolute chromosome pair length} / \text{total length of haploid complement}$), arm ratio (length of short arm/length of long arm) and centromere index ($100 \times \text{length of short arm} / \text{total length of chromosome}$) together with the chromosome classification are given in Table 1. The karyotype (Figure 1A) consists of 10 chromosome pairs of sharply decreasing size. The last pair is strikingly smaller than the others. Pairs 1, 3, 6, and 8 are metacentric. Pairs 2, 4, 5, 7, and 9 are submetacentric and pair 10 is telocentric (Figure 2).

The NORs were examined in 106 metaphase plates derived either from slide preparations silver-stained directly or from preparations silver stained after Giemsa staining. A variable number of one to three Ag-NOR chro-

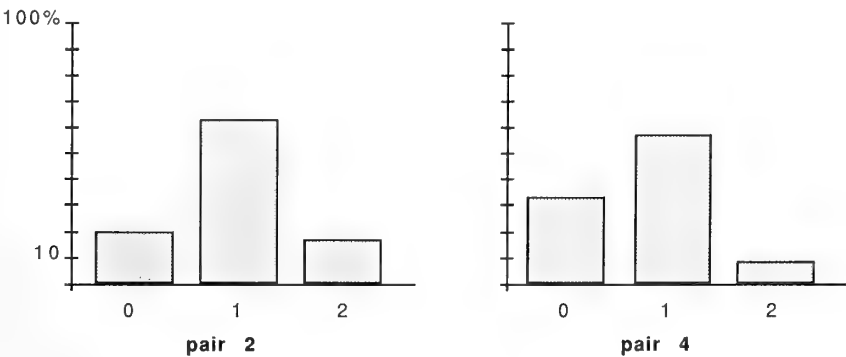


Figure 3

Proportions among cells showing one, two, or zero active NORs after the analysis of 106 metaphase cells in chromosome pairs 2 and 4.

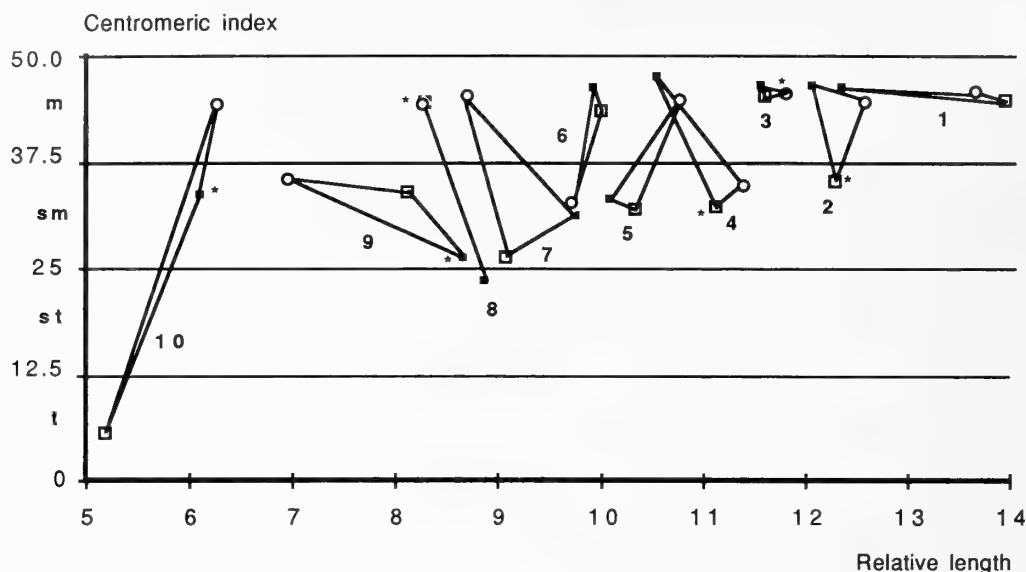


Figure 4

Comparison of morphology and size of the different chromosome pairs in *Ostrea puelchana* (open square), *O. edulis* (black square), and *O. denselamellosa* (open circle). Asterisk indicates Ag-NOR chromosome pair.

mosomes was identified within and between individuals. In all cases, the chromosomal position of the Ag-NOR was found to be terminal on the short arms of the submetacentric pairs 2 and 4. The two homologous chromosomes of these pairs showed heteromorphism involving apparent NOR activity. Figure 3 gives the proportions among cells showing one, two, or zero active NORs in chromosome pairs 2 and 4. The most frequent case (41.51%) was one silver-stained NOR chromosome, simultaneously in pairs 2 and 4.

DISCUSSION

The diploid number of $2n = 20$ observed in *Ostrea puelchana* is common among Ostreacea. The percentage of aneuploid cells scored here is close to that recorded in other ostreid species (THIRIOT-QUIÉVREUX, 1986; INSUA & THIRIOT-QUIÉVREUX, 1991).

Comparison of morphometric measurements of chromosomes in *Ostrea puelchana* (this paper), *O. denselamellosa* (INSUA & THIRIOT-QUIÉVREUX, 1991), and *O. edulis* (THIRIOT-QUIÉVREUX, 1984, table 3) is given in Figure 4. Among these three species, three chromosome pairs (1, 3, and 9) share the same position and the same morphology in the karyotypes. The other pairs overlap two categories of the chromosome classification. Pair 10 is strikingly different among these three species (metacentric in *O. edulis*, submetacentric in *O. denselamellosa*, and telocentric in *O. puelchana*). Thus, *O. puelchana* differs from *O. denselamellosa* and *O. edulis* by the different proportions of metacentric and submetacentric chromosome pairs, and especially by the occurrence of a small telocentric pair.

Comparison of the pattern of Ag-NORs in *Ostrea puel-*

chana (this paper), *O. denselamellosa* (INSUA & THIRIOT-QUIÉVREUX, 1991), and *O. edulis* (THIRIOT-QUIÉVREUX & INSUA, 1992) indicates that (i) the chromosomal location of NORs was different in the three species: terminal on the short arm of submetacentrics in *O. puelchana*, terminal on metacentrics in *O. denselamellosa* and terminal on the long arm of submetacentrics in *O. edulis*, (ii) the position of NORs within karyotypes showed a specific pattern: pairs 2 and 4 in *O. puelchana*, pairs 3 and 8 in *O. denselamellosa* and pairs 9 and 10 in *O. edulis*, allowing identification of chromosomal differences in the morphologically similar pairs 3 and 9, and finally, (iii) heteromorphism involving the apparent NOR activity occurred in the three species.

In conclusion, the karyotype and NOR pattern of *Ostrea puelchana* clearly separate this species from the two other *Ostrea* species previously examined, perhaps giving cytotoxic arguments for the *Ostrea* subdivision (HARRY, 1985) into two subgenera, *Ostrea* s.s. and *Eostrea*.

ACKNOWLEDGMENTS

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Variability in Growth and Age Structure Among Populations of Ribbed Mussels, *Geukensia demissa* (Dillwyn) (Bivalvia: Mytilidae), in Jamaica Bay, New York (Gateway NRA)

by

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Abstract. Growth rates, body weight, density and biomass of ribbed mussels, *Geukensia demissa* (Dillwyn), were determined at *Spartina alterniflora* marsh-flat sites in Jamaica Bay, New York (Lower Hudson Estuary). Cumulative growth and annual growth increments varied but rates were lower at sites within the central bay relative to peripheral sites. Local variability both in size at Ring-1 and size-specific annual growth rates probably account for the variability in cumulative length. No patterns were noted in frequency distributions of shell size but congruence in age structure was observed among neighboring sites in some areas of the bay. Length-specific dry body weights were lower in the central bay. Mussel densities were greater within Jamaica Bay than at most other locations reported in the literature and estimated biomass values were lower. Growth rates of Jamaica Bay mussels were lower than other populations in the northeastern American coast. Four hypotheses that may account for observed *Geukensia* growth rates in Jamaica Bay are presented and discussed: higher population density, higher vertical marsh levels, variability in phytoplankton quality and/or quantity, long-term sublethal chemical pollution.

INTRODUCTION

Jamaica Bay is an urban estuary located at the southwestern end of Long Island and comprises the easternmost component of the Lower Hudson River estuarine system. Bounded on the north by the New York City boroughs of Brooklyn and Queens, and on the east by Long Island's Nassau County, most of the bay at present is included within the Gateway National Recreation Area. In spite of severe human impacts from pollution, development, and population pressure, Jamaica Bay remains a critical local resource for migrating shorebirds and waterfowl and provides nesting sites for several endangered wildlife species.

The intertidal zone of much of Jamaica Bay is bordered by *Spartina* salt marshes. A ubiquitous inhabitant of this community is the Atlantic ribbed mussel, *Geukensia demissa* (Dillwyn, 1817) (BERTNESS, 1984). This bivalve may prove useful as a candidate for long-term monitoring of environmental quality in Jamaica Bay. Its advantages include: (1) Mussels are relatively long-lived (>10 yr at many places) and moderately large (>1 g dry weight); (2) Mussels are relatively immobile (after a post-settlement period of active movement) and accessible year round; (3) The age of individual mussels can be determined by enumeration of external annuli (LUTZ & CASTAGNA, 1980; BROUSSEAU, 1984); and (4) As long-lived filter feeders,

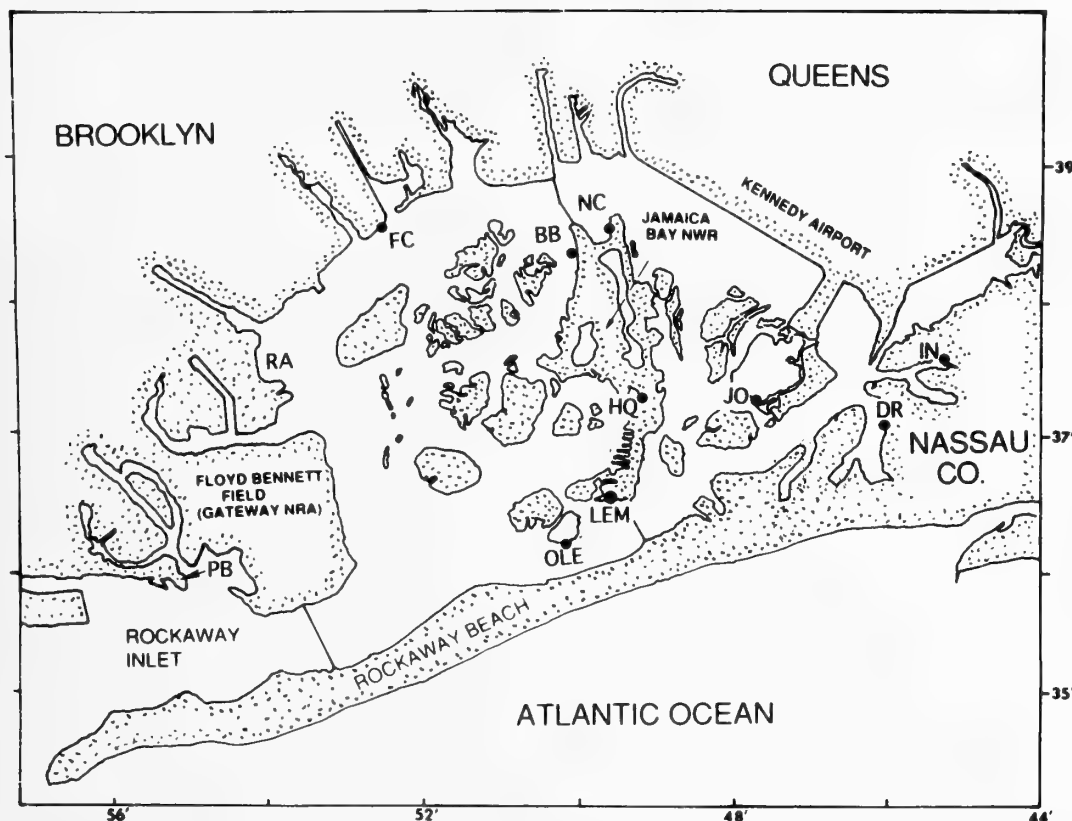


Figure 1

Map of Jamaica Bay (New York City) showing location of mussel sampling sites. W, water; PB, Plum Beach; RA, Riding Academy; FC, Fresh Creek; BB, Black Bank; NC, North Channel; JO, Joco; In, Inwood; DR, Drucker; HQ, Headquarters; LEM, Inner Little Egg; OLE, Outer Little Egg.

mussels may integrate the effects of low concentrations of suspended or dissolved toxic materials, which may be measurable as sublethal modifications of physiological functions such as growth or reproduction. The prerequisite for the use of mussels for this purpose is an adequate understanding of their ecology, particularly the role of natural variables in affecting these physiological functions. The purposes of the research reported here were to determine the variability in *Geukensia* growth rates among sites within Jamaica Bay, and to compare growth with data from other locations.

MATERIALS AND METHODS

Study Sites

Mussel populations (Figure 1) were selected to include a range of habitats within Jamaica Bay as well as a site just outside of the Bay proper (Plum Beach). At all sites, mean tidal range is close to 1.5 m. Sites were visited between June and September 1991. At all locations, collections came from the marsh flat, which is the section of the "tall" *Spartina alterniflora* salt marsh immediately upshore of the marsh edge, and characterized by the presence of

Spartina culms. All marsh-flat samples were collected approximately 1 m from the marsh edge.

Analyses

For analyses of growth, entire sections of turf containing mussels were cut by spade and brought to the laboratory, where larger mussels were removed by hand, and small mussels were washed into a 1-mm sieve. Barnacles and epiphytic growth were scraped from larger mussels, which were scrubbed with a metal brush. Mussels used for age determination were steamed open, the flesh was removed, and the paired valves were numbered. Age was determined by counting external growth annuli following the methods of LUTZ & CASTAGNA (1980) and BROUSSEAU (1984). The growth annulus appears at the time of new growth beginning in May. Transmitted light was used to identify annuli in smaller mussels. Annuli were then confirmed by examination of the outer shell surface under the dissecting microscope. Shells of larger, older mussels were soaked in Clorox to remove the periostracum. The shell length corresponding to each annulus was measured with vernier calipers.

Mussel density (m^{-2}) was estimated at eight sites. Mus-

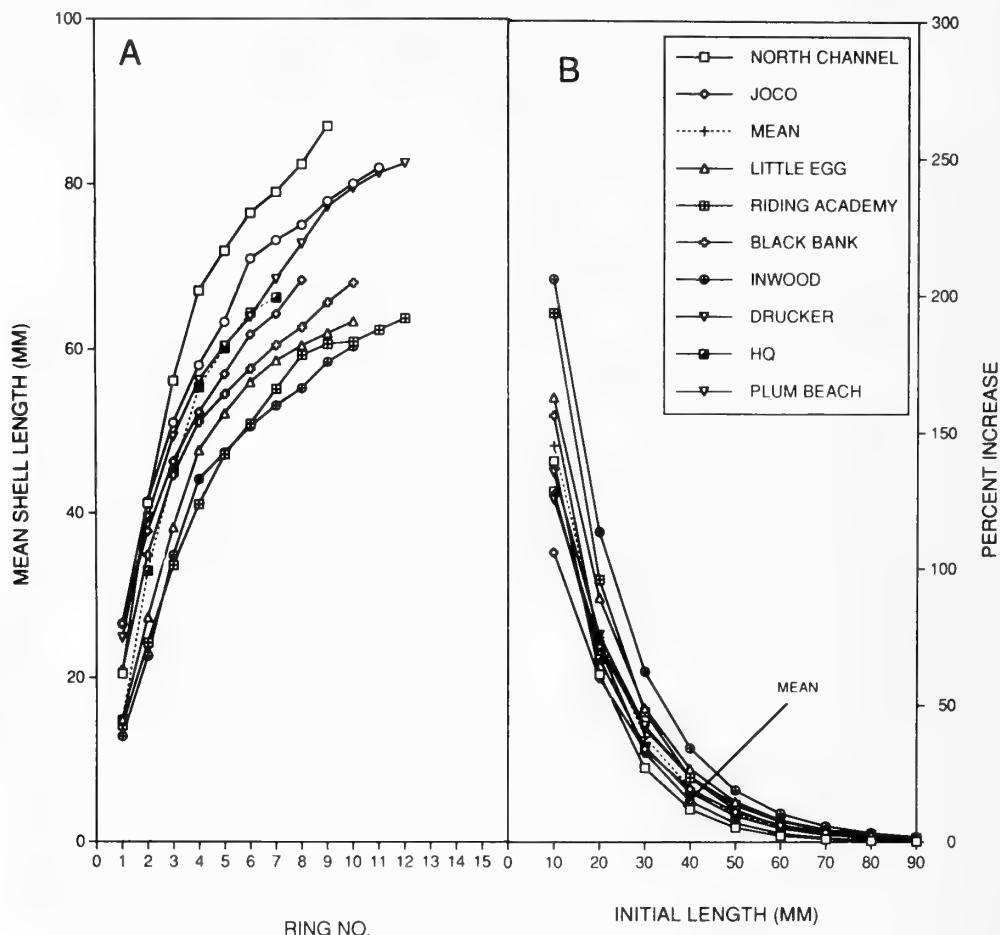


Figure 2

A. Cumulative growth curves of nine mussel populations. B. Fitted size-specific relative growth curves. The y-axis is the log(mean percent annual length increase); x-axis is the initial length of a mussel at the beginning of a growth season. The curve labelled "mean" is generated using regression coefficients averaged for all populations, and may be considered as an average relative growth curve for Jamaica Bay mussels.

sels were counted in 18 circular quadrats (area = 346 cm²) which were located randomly along a line stretched parallel to the marsh edge.

Dry body weight/shell length relationships were determined for six populations in July 1991. For each population, 25 mussels spanning the available size range were selected. After measuring shell length, bodies including fluids were removed by dissection into pre-weighed pans. Tissues were dried at 70°C for 48 hr and re-weighed using a Metler Microbalance. Log-linear regressions of dry weight vs. shell length were used in conjunction with density and size-frequency distributions of mussels to estimate biomass.

RESULTS

Cumulative and Relative Growth

Cumulative growth curves for nine marsh-flat mussel populations from a range of sites within Jamaica Bay

(Figure 2A) show that higher growth rates occurred at sites located away from the central core of the bay (e.g., Inwood, Little Egg Marsh, Plum Beach, and Riding Academy). Lower growth occurred at sites within the central core of the bay (e.g., Drucker Marsh, North Channel Marsh and Black Bank Marsh). Mussel length at year-1 was a poor predictor of size at age-8 ($R^2 = 0.31$, $P = 0.07$) but probably is a factor of importance in determining asymptotic future size. Another factor is the geographical position of the population within the bay.

In order to distinguish between these factors, data from the growth curves in Figure 2A are rearranged in Figure 2B as size-specific relative growth curves—i.e., the annual growth increment as a percentage of length at the initiation of growth for each year. These are fitted curves based on linear regressions of the log[(annual growth/initial length) \times 100] vs. initial length. Initial length is the mean length of an age cohort at the start of any growing season; annual growth is the mean increment in length for the cohort by

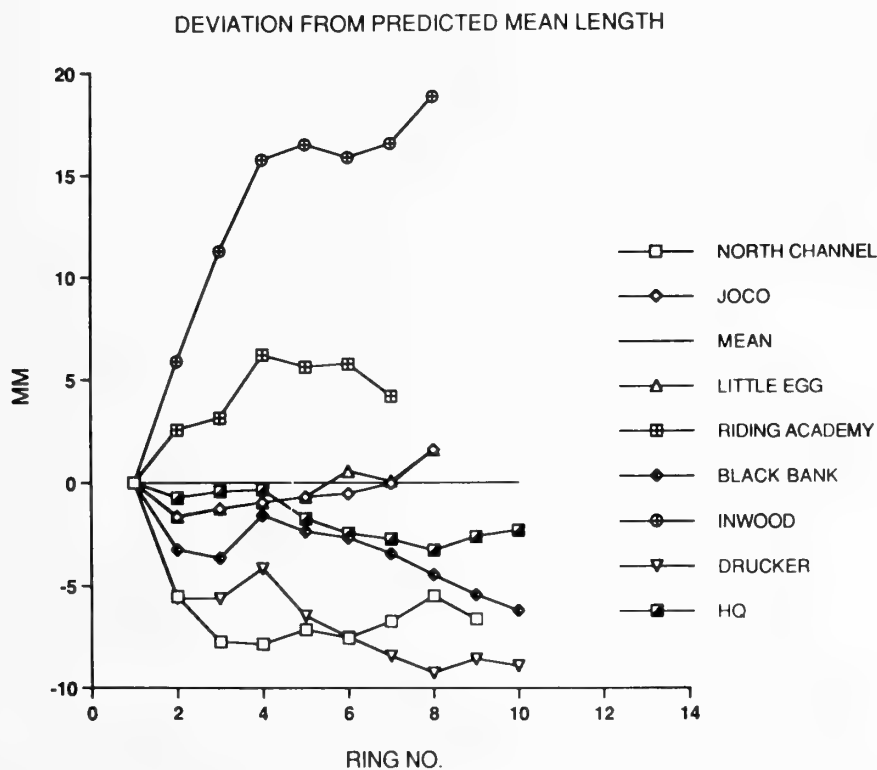


Figure 3

Predicted growth curves for Jamaica Bay populations are generated using observed initial (Ring-1) mean lengths in combination with the "mean" growth coefficients for Jamaica Bay from Figure 2B. If the mean curve accurately portrays growth for Jamaica Bay mussels, observed and predicted growth curves would be identical. Note that observed growth tends to be lower than predicted at sites in the central bay but higher at sites distant from the central core and outside of the bay.

the end of the growing season. Linear regression coefficients used to generate these curves and regression statistics are summarized in Table 1. An average growth curve for all populations (Figure 2B) has been used to reconstruct the cumulative growth curves. The average curve is based on the mean regression coefficients of all populations. These coefficients can then be used to simulate a cumulative growth curve for any site by using the observed mean year-1 length for that site as a starting point. To the extent that the average curve in Figure 2B accurately portrays a generalized growth strategy for Jamaica Bay mussel populations, the resulting "predicted" growth curves should be equivalent to the observed curves. Deviations between the observed and predicted growth curves in relation to age are shown in Figure 3 for each site.

Frequency Distributions of Size and Age

Frequency distributions of age and shell length for all populations are shown in Figure 4. Shell-length distributions are polymodal and variable, with no pattern of similarity among sites. The absence of small mussels at sites such as North Channel and Inwood may indicate scarcity of 1991 and, possibly, 1990 year classes.

Mussel Body Weights, Density, and Biomass

Regression coefficients [$\log(\text{dry weight, g}) = a + b \log(\text{shell length, mm})$] for six populations, and fitted curves reflecting these coefficients are shown in Table 1 and Figure 5. Note that length-specific dry body weight (DW) is highest outside of Jamaica Bay (Plum Beach) and is lower at sites within the central core of the bay (Black Bank, Fresh Creek, Drucker). Mussel density at eight marsh-flat sites (Table 2) ranged between 600 and 1900 m^{-2} .

Estimates of biomass (g DW m^{-2}) for eight marsh-flat populations (Table 2) show that biomass ranged from 0.21 kg (Drucker) up to 0.46 kg (Plum Beach). At sites within Jamaica Bay, biomass ranged from 0.21 to 0.42 kg.

DISCUSSION

Mussel populations in the central core of Jamaica Bay exhibit lower growth in comparison with more distant sites within the bay and with other locations in the northeastern American coast. This can be seen most clearly in the comparison between observed relative growth curves and predicted curves based on average growth statistics for all populations (Figure 3). Although the observed and pre-

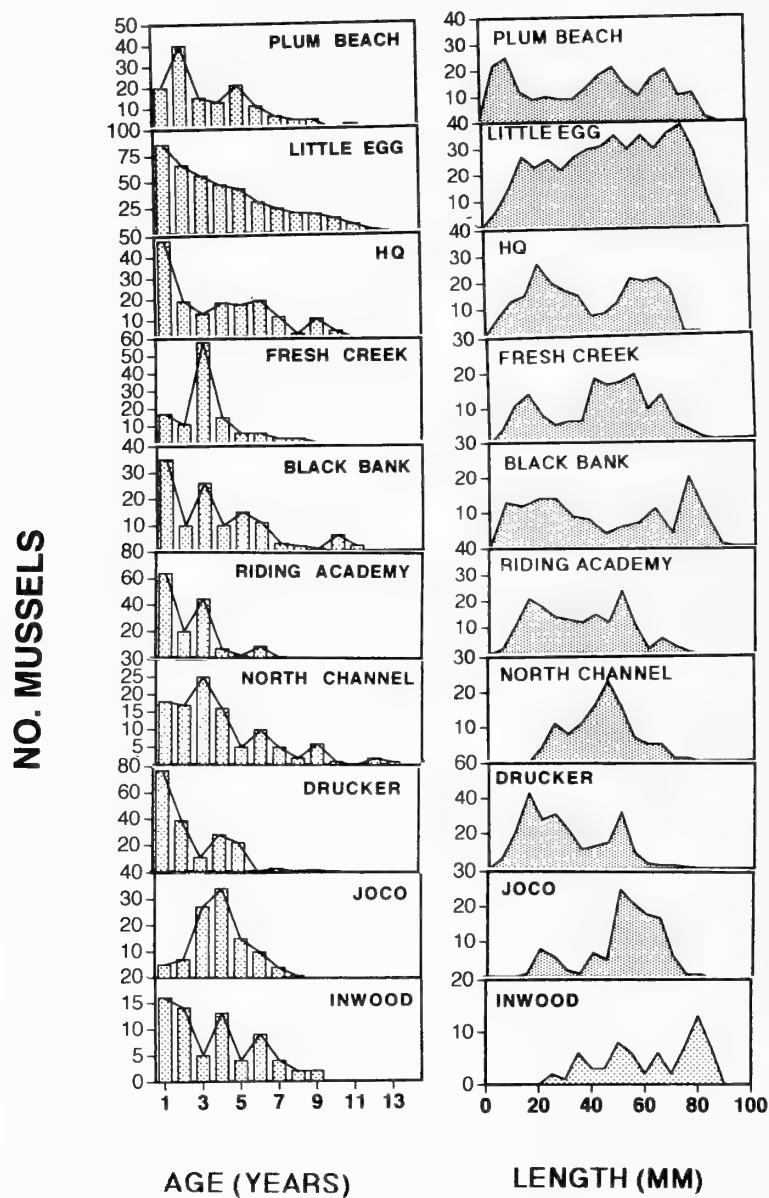


Figure 4

Left panel shows age structure of each population (excluding 1991-class mussels). Right panel shows shell length-frequency distributions at all sites based on collections taken between June and September 1991.

dicted curves are similar at some sites (HQ, Little Egg, Joco), the predicted curves deviate from the observed curves at others. If cumulative growth curves were determined primarily by size at year-1, then the pattern of deviation relative to geographical location should be random. However, this clearly is not the case (Figure 3). At sites closer to the entrance to Jamaica Bay (Plum Beach, Riding Academy) the observed growth curves exceed the predicted. At sites in the central bay (HQ, North Channel, Drucker, Black Bank) the observed growth is lower than the predicted. Growth rates at the Inwood site are anomalously

high. However, this population is located within the warm-water plume of an electric generating station. These data suggest that mussel populations in the central bay may be more stressed than populations located peripherally, as reflected by a smaller annual proportional allocation to growth—*i.e.*, mussels of any given size in the central bay increase in size by a smaller percentage of starting size per year than other populations.

Although no patterns in population size structure were discernible, there was congruence in age composition between some sites. For example, all of the northern sites

Table 1
Regression statistics for *Geukensia demissa*.

A. Regression statistics: log(annual length increment/initial length) vs. initial length.

Site	b	a	r ²
North Channel	-0.035	0.499	0.83
Little Egg	-0.026	0.473	0.94
Black Bank	-0.034	0.532	0.97
Drucker	-0.032	0.382	0.96
Inwood	-0.025	0.572	0.98
Joco	-0.025	0.271	0.94
Riding Academy	-0.03	0.591	0.96
HQ	-0.028	0.39	0.88
Plum Beach	-0.024	0.338	0.93

B. Regression statistics: log(dry weight, g) vs. log(length, mm)

Site	b	a	r ²
Black Bank	2.837	-5.342	0.99
Drucker	3.177	-5.947	0.97
Joco	2.557	-4.805	0.97
HQ	2.43	-4.416	0.95
Plum Beach	2.893	-5.189	0.98
Fresh Creek	2.742	-5.168	0.99

(Riding Academy, Fresh Creek, North Channel, and Black Bank) show a pulse of 3-year mussels, suggesting that all received relatively large numbers of recruits in the 1989 season. Since these sites are fairly distant from the entrance to the bay (Rockaway Inlet), which is the only external source of larvae, these recruits probably originated within Jamaica Bay. At Plum Beach (outside of Jamaica Bay) and at the Little Egg and HQ sites, more age classes are represented with less year-to-year fluctuation in numbers over time than at other sites within Jamaica Bay. These sites, located nearer the inlet, are more likely to receive larvae brought into the bay with tidal currents and may be less dependent on localized recruitment than sites in the central and eastern bay.

Table 2
Mussel density and biomass at eight sites.

Site	Density (m ⁻²)				Biomass (g/m ²)	
	Mean	SE	No. quad- rats	CV†		ID‡
North Channel	919	159	18	73.5	496	226.7
Little Egg	622	72	18	49.4	151	308.4
Black Bank	1888	173	16	36.5	252	379.5
Drucker	1955	138	18	30	176	214.7
HQ	1545	85	15	21.4	71	418.7
Plum Beach	735	111	8	42.8	135	463.1
Outer Little Egg	1215	93	18	32.4	127	379.8
Fresh Creek	802	109	18	57.8	268	218.2

† CV = Coefficient of variation = (SD/mean) × 100.

‡ Index of dispersion = variance/mean.

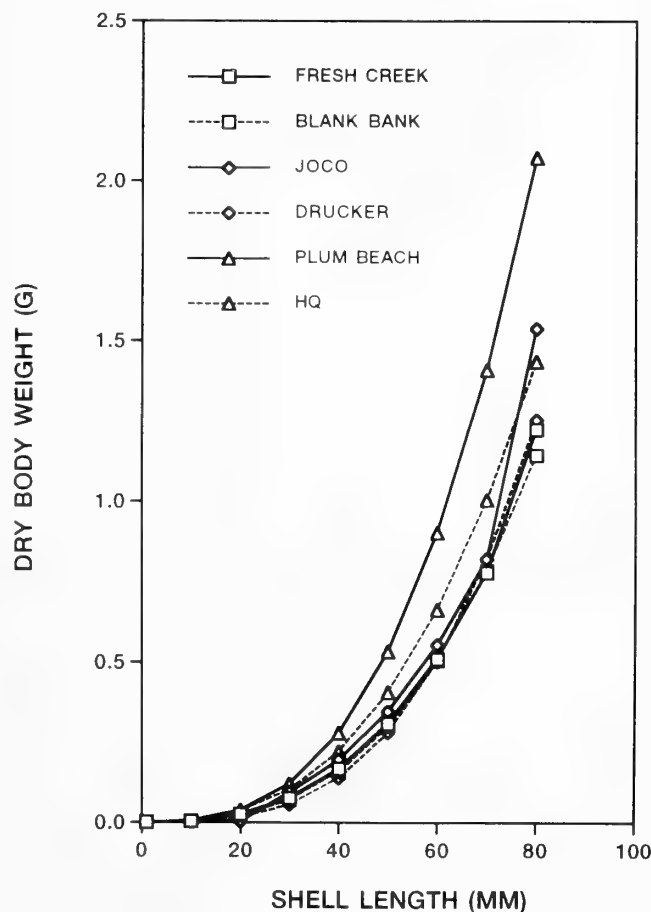


Figure 5

Fitted curves showing the relation between dry body weight (g) and shell length (mm) for six sites in July 1991. Note that body weights tend to be lower in populations from central Jamaica Bay. Curves are produced using linear regression coefficients for the equation: $\log(DW) = a + b(\log \text{ length})$.

Population density (Table 2) was variable and all populations were highly clumped. Coefficients of variability ($CV = SD/\text{mean} \times 100$) ranged from 21 to 73% and coefficients of dispersion ($CD = s^2/\text{mean}$) ranged from 71 to 496. Densities were statistically different among Jamaica Bay sites (Kruskal-Wallis statistic = 48.91, $P < 0.001$) and fell within the range of maximum *Geukensia* densities reported by others working in the New England to northern Middle-Atlantic region (FELL *et al.*, 1982; BERTNESS, 1984; BERTNESS & GROSHOLZ, 1985). Comparing density data between studies is problematic; however, the Jamaica Bay marsh flat densities seem much greater than those in the eastern Long Island Sound marshes investigated by FELL *et al.* (1982) but similar to the western Long Island Sound marshes (and to the Narragansett Bay site studied by BERTNESS, 1984).

Estimates of biomass for Jamaica Bay mussel populations were lower than those reported by FELL *et al.* (1982) for the Great Meadows and Branford marshes in west-

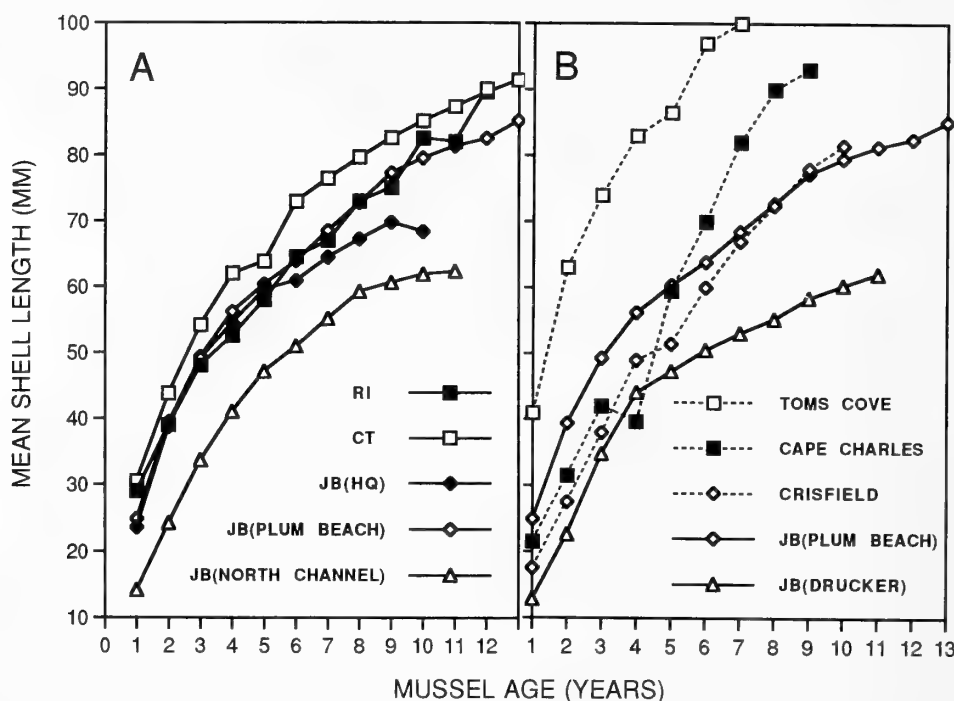


Figure 6

A. Cumulative growth curves for two within-bay sites (HQ, North Channel) and a site from the Rockaway Inlet outside Jamaica Bay (Plum Beach) compared with literature data for Rhode Island (BERTNESS & GROSHOLZ, 1985) and Connecticut (BROUSSEAU, 1984). Note that within-bay sites show lower growth rates.

B. Similar data comparing Jamaica Bay and Rockaway Inlet sites with published growth curves for three sites inside and outside of Chesapeake Bay (curves redrawn from BERTNESS, 1980). Note that the within-bay site (represented here by Drucker) is lower than all Chesapeake sites, but that growth at Plum Beach (outside of Jamaica Bay) is similar to the Crisfield site (within Chesapeake Bay).

ern Long Island Sound. There was no statistically significant correlation between mussel density and biomass in Jamaica Bay, whereas these appear to be positively correlated in the Connecticut marshes studied by FELL *et al.* (1982). This suggests that environmental factors in addition to crowding determine mussel biomass in Jamaica Bay.

There are few appropriate data on the growth rates of *Geukensia demissa* that can be compared with Jamaica Bay. In Figure 6, growth curves of Jamaica Bay mussels are superimposed on published growth curves for mussels from Connecticut (BROUSSEAU, 1984), Rhode Island (BERTNESS & GROSHOLZ, 1985), and the Chesapeake Bay area (BERTNESS, 1980). The New England mussel populations (Connecticut, Rhode Island) have higher growth rates than all inter-Jamaica Bay populations, but are similar to Plum Beach (Figure 6a). However, all of the Chesapeake Bay area populations exceed Jamaica Bay growth rates, including the Crisfield site, located well within Chesapeake Bay. BERTNESS (1980) suggested that differences in growth rates in his study reflected habitat-related physical differences among sites, including food quantity and quality.

Our results indicate that the mussels at Plum Beach (outside of Jamaica Bay) grew at rates comparable to those

in other northeastern American populations. However, mussels within Jamaica Bay grew more slowly, and size-specific body weights of mussels in central bay populations were depressed relative to mussels in populations in the Rockaway Inlet (Plum Beach).

We propose and briefly discuss four hypotheses which, either singly or in combination, may account for depressed growth rates within Jamaica Bay: (1) Mussels in the central core of Jamaica Bay may be more crowded than in populations outside of the bay; (2) The vertical shore level of the marsh flat at sites within Jamaica Bay may be higher than at sites outside of Jamaica Bay; (3) Mussel populations within Jamaica Bay may utilize a qualitatively and/or quantitatively different phytoplankton population from mussels populations outside of Jamaica Bay; (4) Mussel populations in Jamaica Bay may be stressed as a result of long-term exposure to toxic heavy metals, polyaromatic hydrocarbons, or other chemical pollutants.

By experimentally manipulating mussels in the size range of 30 to 100 mm, BERTNESS & GROSHOLZ (1985) were able to show that mussels at high experimental densities (1600 m^{-2}) grew more slowly than mussels at low density (400 m^{-2}). However, the crowding effect on growth was smaller than the effect of shore level—*i.e.*, in spite of greater

crowding, mussels at the marsh edge, which could filter for longer periods on each tidal cycle, grew faster than marsh flat mussels in the low density treatment. These results indicate that crowding will negatively affect growth, but that the crowding effect may be relatively small compared to the effect of shore level. As noted above, Jamaica Bay sites support relatively dense populations. Moreover, there is a statistically significant inverse correlation between mussel length at year-7 and mean density ($r = -0.71$, $P = <0.05$). These results are consistent with the hypothesis of density-dependent depression of growth rates in Jamaica Bay. However, neither the sampling methods used in this study nor the numbers of samples collected were appropriate to test adequately this hypothesis.

During this study, we observed that the vertical level of the marsh edge varies significantly among sites owing to differences in erosion and sediment deposition. On the basis of work by BERTNESS & GROSHOLZ (1985), noted above, as well as other unpublished data from Jamaica Bay, we suggest that this factor could account for some of the variability in mussel growth rates among sites, although this might not explain the general depression of growth rates within the central bay.

Available evidence on the species composition and productivity of phytoplankton in Jamaica Bay (PETERSON & DAM, 1986) is consistent with similar investigations in the Lower New York Harbor and New York Bight (MALONE, 1977), and indicates that plankton populations shift from diatom-dominated assemblages in early spring to nanoplankton (especially phytoflagellate)-dominated assemblages in summer. Other studies (PETERSON *et al.*, 1985) indicate that *Geukensia* populations located deeper within marsh-dominated estuaries may utilize greater amounts of detrital material than populations associated with the major marsh creeks and inlets, which consume larger amounts of phytoplankton. Accumulating evidence (*e.g.*, STIVEN & KUENZLER, 1979; FRECHETTE & BOURGET, 1985) supports a conclusion that some mussel populations may be food limited. Although there is no evidence at present that site differences in potential food quality in Jamaica Bay account for differences either in growth or individual body weight, this topic requires further study. Spatial variability in current velocities also may relate to food abundance and quality. However, tidal current velocities are high in Jamaica Bay, and at present we have no evidence suggesting a correlation between flow rates and mussel growth.

Jamaica Bay receives relatively large loadings of nutrients, heavy metals, PAHs, and other chemicals from many point and non-point sources, including two sewage treatment plants, large volumes of combined sewer overflows, run-off from Kennedy International Airport, and chemical leachates from three inactive municipal landfills (FRANZ & HARRIS, 1988). Mussels (*Mytilus edulis*) sampled from Jamaica Bay in the Mussel Watch Program (NOAA, 1989)

exhibited high tissue concentrations of several toxic metals, PAHs and PCBs, some of which may induce sublethal stress in mussels. The possibility that depressed growth of *Geukensia* may be caused by chemical pollutants needs further investigation.

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Maturation Processes in Female *Loligo bleekeri* Keferstein (Mollusca: Cephalopoda)

by

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Abstract. Maturing oocytes of the squid *Loligo bleekeri* were cytologically described depending on the degree of formation and development of oocytes and associated follicle cells. Sexual maturity was defined with histological observations and divided into five phases: Phase I-V. The composition of oocytes in ovaries revealed that oocyte development was highly asynchronous. Seasonal changes of the five phases of maturity revealed that the final maturation of *L. bleekeri* was completed in a short period of its life history.

INTRODUCTION

The maturation process in squid has been studied in various species, including *Loligo pealei* (SELMAN & ARNOLD, 1977), *L. opalescens* (KNIPE & BEEMAN, 1978), *L. vulgaris* (SAUER & LIPINSKI, 1990), *Lolliguncula brevis* (COWDEN, 1968), and *Todarodes pacificus* (TAKAHASHI & YAHATA, 1973; IKEDA *et al.*, 1991). In particular, SELMAN & ARNOLD (1977), using both light and electron microscopical techniques, defined distinct maturation stages according to the structure of the follicle.

Loligo bleekeri is endemic to the western North Pacific and is one of the few loliginid squids adapted to cool water (NATSUKARI & TASHIRO, 1991). A number of ecological and biological aspects of the species have been investigated by various researchers (for review of the literature see NATSUKARI & TASHIRO, 1991): distribution, migration, growth and life span based on the statolith analysis, maturation, and reproduction (including mating and spawning behavior, spawning season, and spawning ground). A Gonado-somatic Index or the color and thickness of the reproductive organs were recommended as the best indices of sexual maturity in *L. bleekeri* because they are easily determined, even though no histological evidence has been presented. In *L. bleekeri*, there is no information on the maturation process based upon histological observation.

The purpose of our study is to describe the maturation

process in *Loligo bleekeri*, based upon cytological and histological observation.

MATERIALS AND METHODS

Specimens of *Loligo bleekeri* in northern Japan were collected by set nets or bottom trawls from the coastal waters of southern Hokkaido: Usujiri; Fukushima; Matsumae (local spawning ground), and the coast of Azigasawa, during 1990 and 1991 (Figure 1). For this study, a total of 108 females ranging from 68 to 282 mm in dorsal mantle length (ML) were used. Reproductive organs and total body were weighed in order to calculate the Total Gonadosomatic Index: $TGSI = [(ovary\ wt + oviduct\ (+\ gland)\ wt) / body\ wt] \times 100$. Length was measured as ML. Ovaries (108), fixed in Bouin's solution, were sliced at 6-7 μm in thickness. For observation, sections were stained with Delafield's hematoxylin and eosin. The Periodic Acid-Schiff (PAS) technique was utilized to stain for polysaccharides.

In *Loligo bleekeri*, the appropriate maturity index is TGSI rather than GSI, because when a female becomes sexually mature, ripe eggs are released from the ovary and are stored in the oviduct until egg-laying occurs. Serial tissue slices for each specimen were obtained, a well-formed slice was selected, maturity was determined, and the composition of germ cells at each phase of sexual maturity was

calculated by counting the germ cells (those having their nuclei and being in good condition) at various stages.

RESULTS

General Anatomy of the Ovary

The ovary of *Loligo bleekeri* lies in the coelomic space at the apex of the mantle and is suspended by connective tissue mid-laterally and dorso-posteriorly. The ovarian structure consists of a main axis of central connective tissue with a large number of branches. Germ cells are clustered around the branches of connective tissue like bunches of grapes.

Cytological Description of Maturing Oocytes

Oocytes were conveniently distinguished into eight stages (stage 1–8) based upon the degree of formation and development of the oocytes and associated follicle cells. Oocytes at various stages were described below.

Stage 1. Oogonium production (Figure 2A): Secondary oogonia (ca. 35 μm in the long axis) have a well-defined germinal vesicle (ca. 27 μm) surrounded by a thin layer of pale-staining cytoplasm. The large nucleus contains scattered chromatin materials.

Stage 2. Primary growth (Figure 2B, C): The youngest oocytes are ca. 50–80 μm in diameter. The centrally located nuclei (ca. 40–45 μm) usually possess several prominent spherical and irregularly shaped nucleoli (ca. 5–7 μm). One or two squamous follicle cells are attached to the surface of the growing oocyte. The follicle cells are ca. 12 μm and the oocytes ca. 140–220 μm in diameter. Attachment and multiplication of a follicular cap appeared to develop first at the vegetative pole of the oocyte. A large nucleus (ca. 70–100 μm) is surrounded by an irregular corona.

Stage 3. Follicle cell multiplication (Figure 2D): A contiguous layer of follicle cells has completely surrounded the oocyte (ca. 220–330 μm). The follicle cells continue to increase in number, and change from squamous to columnar in shape. Red stained blood vessels are observed on the follicular epithelium. Each developing oocyte is surrounded by supportive connective tissue.

Stage 4. Early yolkless (Figure 2E): The definitive follicular epithelium begins to penetrate the oocyte. The nucleus moves toward the future animal pole of the slightly elliptical-shaped oocyte. Folds of follicle cells, which enclose connective tissue and blood vessels, progressively invade the growing oocyte, with a high mitotic rate.

Stage 5. Late yolkless (Figure 2F, G): The follicle cells, which show cytoplasmic basophilia, continue to elongate. Large multiple nucleoli appear irregularly oval, with a length of approximately 7 μm (nuclei ca. 16 μm). Individual follicle cells are no longer distinguished. A follicular

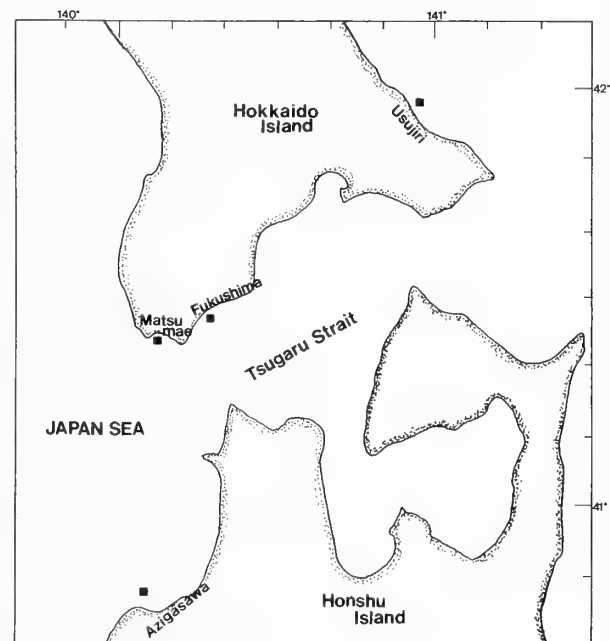


Figure 1

Sampling locations for specimens of *Loligo bleekeri* caught by set nets or bottom trawls. Azigasawa (September 1991); Usujiri (October–November 1990, 1991); Fukushima (December 1990, 1991); Matsumae (December–February 1990, 1991).

syncytium, which reaches a maximum height of ca. 55 μm , is formed.

Stage 6. Early vitellogenesis (Figure 2H): The follicular syncytium is engaged in vitellogenesis and the formation of a chorion. Red-stained yolk bodies are distributed randomly in clusters in the oocyte. Yolk granules are numerous and generally appear as contiguous polyhedra (ca. 15–25 μm).

Stage 7. Late vitellogenesis (Figure 2I, J): The follicular syncytium is displaced toward the periphery of the oocyte by the formation of the PAS-positive yolk mass. Chorionic particles accumulate in the interface between the follicular epithelium and the oocyte as discrete droplets and exhibit a vivid PAS reaction. By the end of this stage, oocytes are ca. 2.2 mm in length, and a thin cytoplasm encloses the yolk mass. Vitellogenesis terminates.

Stage 8. Maturation and ovulation (Figure 2K, L): The formation of the chorion (ca. 37–40 μm thick) is complete. The follicular syncytium has undergone a final degeneration. Mature oocytes (ca. 2.6–2.7 mm in length) are ready to be released or have already been ovulated.

Description of Sexual Maturity

The maturity of *Loligo bleekeri* was divided into five phases on the basis of the stage of the most advanced oocytes in ovaries because oocyte development of the species is

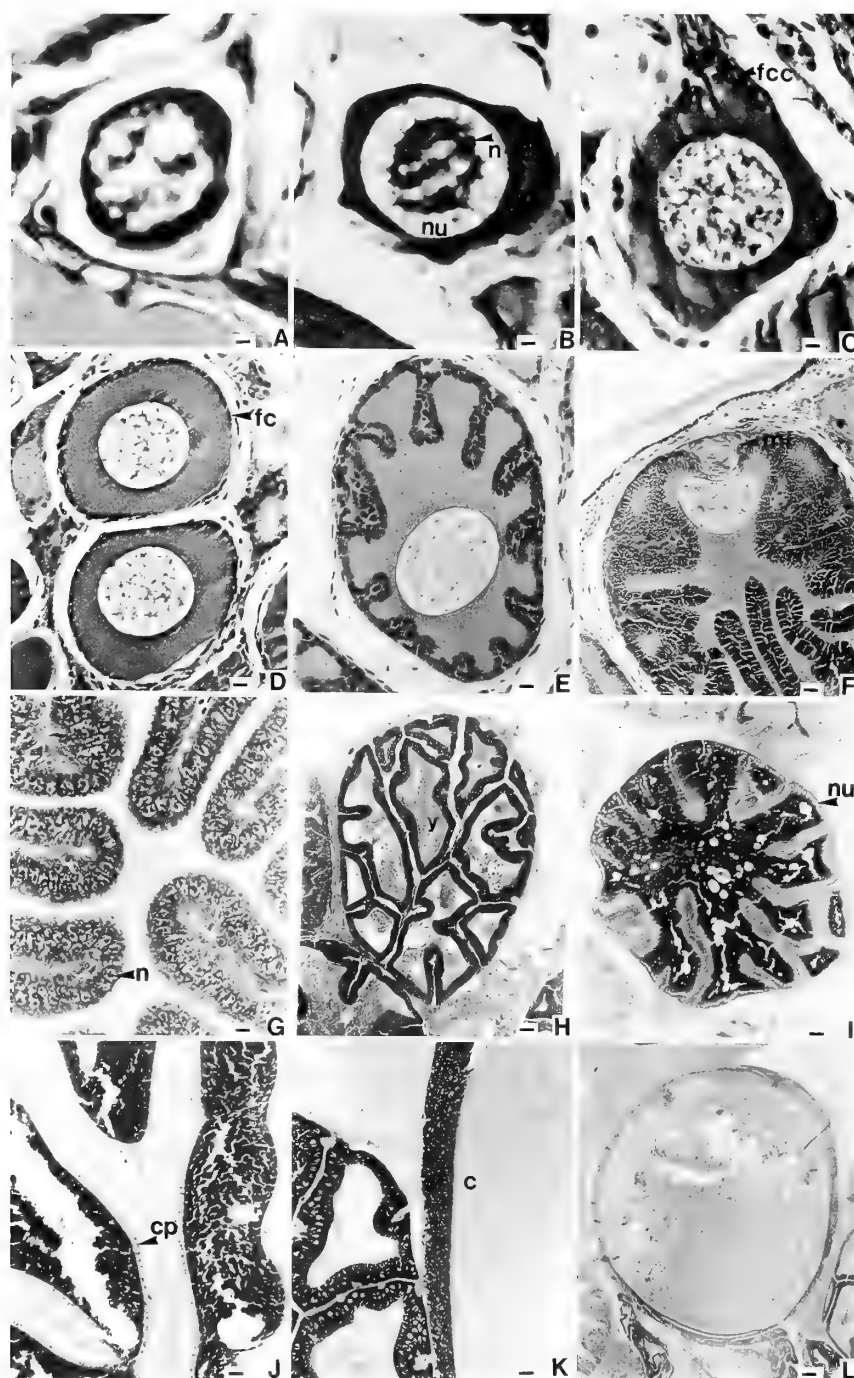


Figure 2

Photomicrographs of germ cells in female *Loligo bleekeri* at various stages of development. A (stage 1). Germ cell at the oogonium production stage, scale line 2.6 μm . B, C (stage 2). B. Young oocyte at the primary growth stage. Large nucleus (nu) contains several prominent spherical and irregularly shaped nucleoli (n), scale line 5.6 μm . C. Oocyte at the late primary growth stage. Follicle cell cap (fcc) on vegetative pole, scale line 11 μm . D (stage 3). Oocytes at the follicle cell (fc)-multiplication stage, scale line 25 μm . E (stage 4). Oocyte at the early yolkless stage. Invagination of follicular epithelium begun, scale line 17.9 μm . F, G (stage 5). F. Oocyte at the late yolkless stage. Micropyle lens (ml), scale line 20.9 μm . G. Follicular syncytium is formed with large nuclei and irregularly oval nucleoli (n), scale line 20.9 μm . H (stage 6). Oocyte at the early vitellogenesis stage. Yolk granules (y), scale line 62.5 μm . I, J (stage 7). I. PAS positive oocyte at the late vitellogenesis stage. Nucleus (nu) of follicular syncytium,

Table 1

Maturation changes during the eight stages of oocyte development in female *Loligo bleekeri*.

Date	ML (mm)	TGSI (%)	Matu- rity phase	Stage of oocyte development (%)								Ovula- tion
				1	2	3	4	5	6	7	8	
11 Sep 91	68	0.18	I	+	100.00							—
11 Sep 91	76	0.17	I	+	100.00							—
11 Sep 91	103	0.16	I	+	100.00							—
10 Oct 90	133	0.27	II	+	37.97	62.03						—
29 Oct 91	183	0.47	II	+	42.53	57.47						—
21 Nov 90	174	0.39	II	+	35.87	64.13						—
29 Oct 91	173	0.19	III		3.61	66.27	24.10	6.01				—
21 Nov 90	163	0.78	III		2.20	36.26	39.56	21.98				—
14 Dec 91	184	1.08	III			38.78	30.61	30.61				—
14 Dec 91	182	1.65	IV			2.56	61.54	17.94	10.26	7.70		—
14 Dec 91	177	1.84	IV			6.67	45.00	35.00	6.67	6.66		—
06 Dec 90	223	4.28	IV				48.72	33.33	7.70	10.25		—
06 Dec 90	244	8.25	V				15.00	35.00	10.00	40.00		+
06 Dec 90	223	12.67	V				1.43	3.33	42.86	52.38		+
20 Dec 90	241	8.75	V				3.45	7.66	22.22	66.67		+
30 Jan 91	264	8.49	V				16.00	32.00	12.00	40.00		+
20 Dec 90	259	10.43	V				5.71	7.62	6.67	66.67	13.33	+
30 Jan 91	263	9.56	V				2.93	7.70	12.22	72.22	5.56	+
20 Feb 91	214	9.25	V				6.67	6.67	6.67	75.23	4.76	+
20 Feb 91	209	7.25	V				17.39	30.43	8.70	36.07	7.41	+

ML: Dorsal mantle length; TGSI: Total gonado-somatic index.

asynchronous. The oocytes used as phasing criteria followed those of SELMAN & ARNOLD (1977). Table 1 reveals the stage composition of oocytes in ovaries of maturing females. All oocytes at the primary growth stage (stage 2) gradually transferred to ones at the more advanced stages during maturation, and, consequently, oocytes in the earlier stages as well as oogonia were not found in the ovaries of fully mature females.

Phase I (Figure 3A, Table 1): The most advanced oocytes are at the primary growth stage (stage 2). A few germ cells at the oogonium production stage (stage 1) are found.

Phase II (Figure 3B, Table 1): The most advanced oocytes are at the follicle cell-multiplication stage (stage 3). The number of oogonia and oocytes at the primary growth stage (stage 2) have decreased prominently. Most oocytes are in the follicle cell-multiplication stage.

Phase III (Figure 3C, Table 1): The most advanced oocytes are at the late yolkless stage (stage 5). The number of oocytes at the follicle cell-multiplication stage (stage 3) has diminished with maturation. Oocytes in the primary growth stage (stage 2) still exist in low numbers. Recruitment to the primary growth stage is completed and oogonia are no longer observed.

Phase IV (Figure 3D, Table 1): Oocytes in various stages coexist in different proportions in the ovary. Oocytes in the late vitellogenesis stage (stage 7) are the most developed. Oocytes at the primary growth stage (stage 2) and follicle cell-multiplication stage (stage 3) are rarely or never found. Most oocytes at the follicle cell-multiplication stage have developed to the yolkless stage.

Phase V (Figure 3E, Table 1): Oocytes in various stages from the follicle cell-multiplication stage (stage 3) to the maturation and ovulation stage (stage 8) coexist in the ovary; however, oocytes at the follicle cell-multiplication stage are never found and oocytes at the early yolkless stage (stage 4) are observed in relatively low numbers. Recruitment to the follicle cell-multiplication stage does not occur, owing to the absence of oocytes at the primary growth stage (stage 2).

Seasonal Changes of the Maturity Composition

Figure 4 indicates the phase of maturity of *Loligo bleekeri* specimens collected periodically. Females at phase I were identified in September. The females had a mean ML of 92 mm and showed a very low TGSI (Table 2). The modal size of females at phase II was between 99 and 177 mm,

scale line 83 μ m. J. Chorionic particles (cp) at the interface region, scale line 20.9 μ m. K, L (stage 8). K. Degenerating follicular syncytium (df) and completed chorion (c), scale line 20.9 μ m. L. Ripe oocyte, scale line 125 μ m.

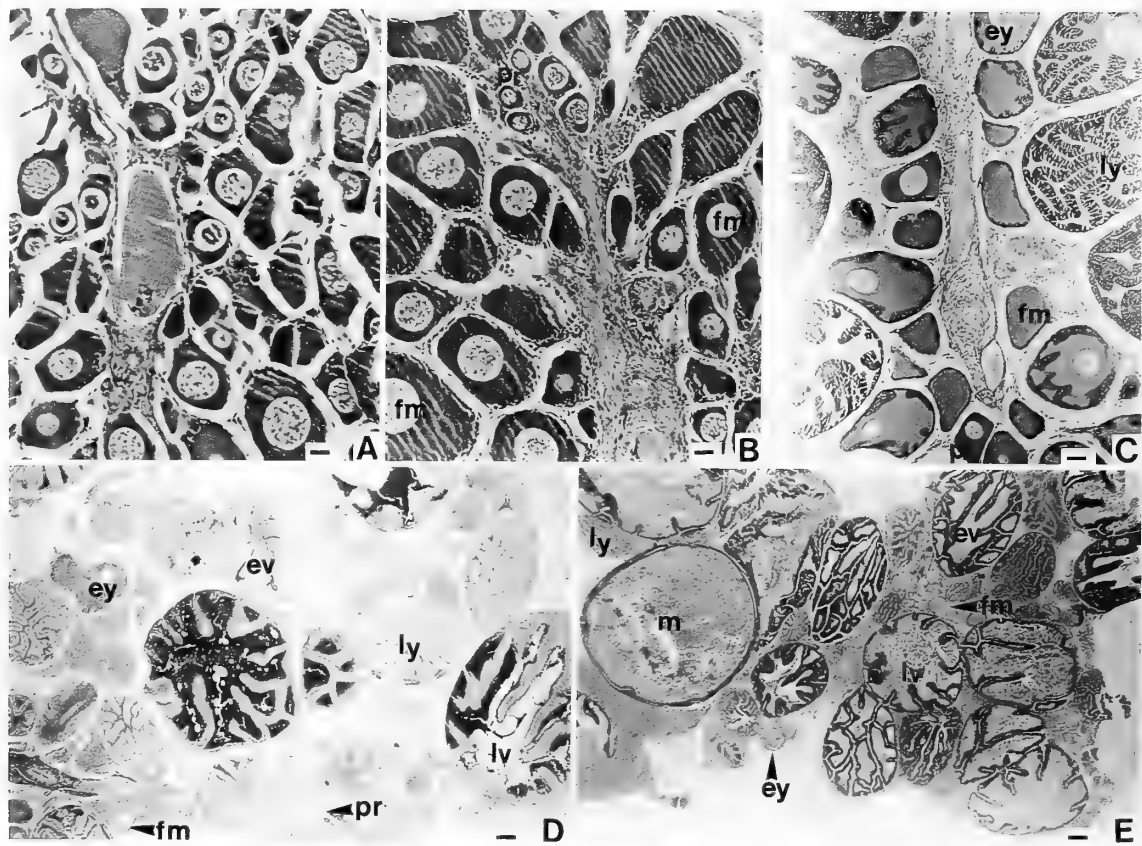


Figure 3

Photomicrographs of cross sections through ovaries in the various stages of maturity. A (phase I). Scale line 41.7 μm . B (phase II). pr, oocyte at the primary growth stage (stage 2); fm, oocyte at the follicle cell-multiplication stage (stage 3), scale line 41.7 μm . C (phase III). ey, oocyte at the early vitellogenesis stage (stage 4), ly, oocyte at the late vitellogenesis stage (stage 5), scale line 41.7 μm . D (phase IV). ev, oocyte at the early vitellogenesis stage (stage 6), lv, oocyte at the late vitellogenesis stage (stage 7), scale line 238 μm . E (phase V). m, oocyte at the maturation and ovulation stage (stage 8), scale line 277.8 μm .

and the TSGI composition of the females showed a slight increase. This phase of maturity appeared in middle September and extended to late November. Phase III appeared first in late October and predominated through November. Phase III females showed a wide range of variation in length composition and a continuous increase in TSGI value. Phase IV was found from late November to middle December. This is an indication that active vitellogenesis is completed in a very short period. Phase IV females showed a significant increase in their TSGI value compared with that of the previous phase and ranged in ML from 177 to 233 mm. Squids at phase V were the major components of the population on the spawning ground. Phase V females were found from December to February, revealed a high TSGI with extreme fluctuations, and showed a significant increase in ML composition.

TSGI and ML values of females at the various phases of maturity were plotted in Figure 5. Although modal size at each phase overlapped, TSGI composition was clearly

separated between females at phases I–III and at phases IV–V. Female *Loligo bleekeri* at phases IV–V are defined by TSGI values greater than 1.5% and ML greater than 175 mm. Phase V females of *L. bleekeri* are easily distinguished by the presence of ripe eggs in the oviduct.

DISCUSSION

The pattern of oocyte development observed in *Loligo bleekeri* is nearly identical to those of *Lolliguncula brevis* (COWDEN, 1968), *Loligo pealei* (SELMAN & ARNOLD, 1977), *Loligo opalescens* (KNIPE & BEEMAN, 1978), and *Loligo vulgaris* (SAUER & LIPINSKI, 1990). Oogenesis in cephalopod mollusks involves a highly coordinated differentiation of the oocyte and follicular epithelium (SELMAN & ARNOLD, 1977). Several morphological and histological studies have elucidated the functions of follicle cells in mollusks: vitellogenesis (O'DOR & WELLS, 1973, 1975; SELMAN & WALLACE, 1978); the formation of the second-

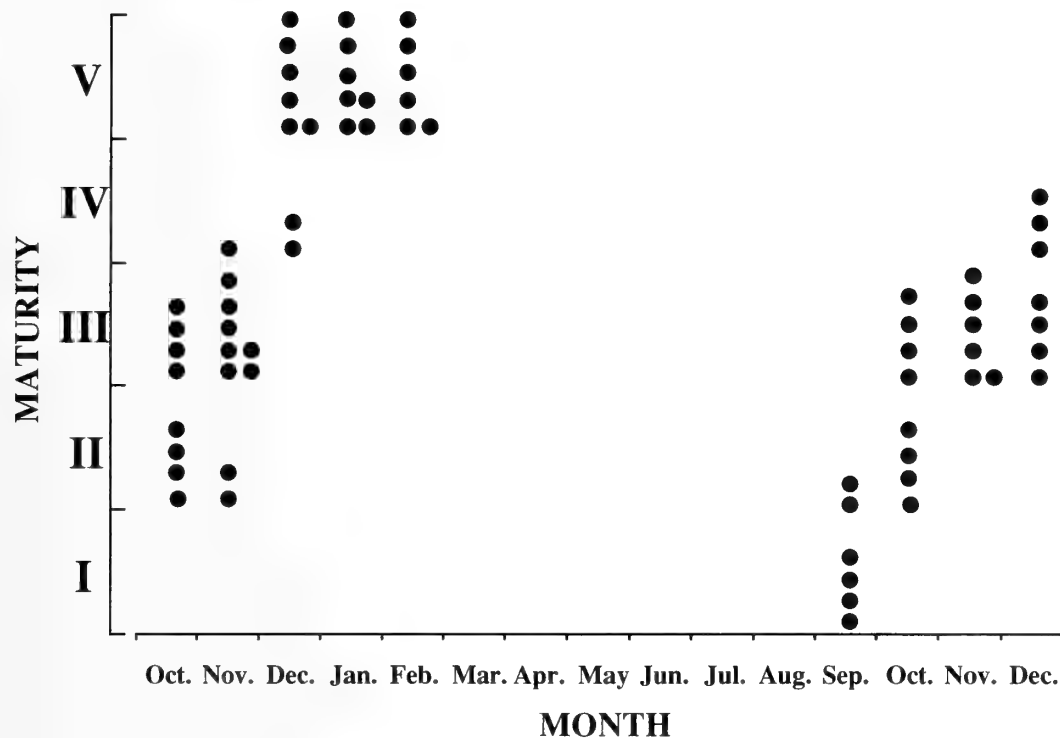


Figure 4

Seasonal changes of the five phases of maturity in female *Loligo bleekeri*.

ary egg membrane (SELWOOD, 1968, 1970; BOTTKE, 1974; SELMAN & ARNOLD, 1977); the ovulation process (DE JONG-BRINK *et al.*, 1976); phagocytosis (SELWOOD, 1968, 1970); hormone production (RUNHAM *et al.*, 1973); the origins of the animal-vegetal and bilateral symmetries of the egg (RAVEN, 1966); and transportation of the oocyte (DE JONG-BRINK *et al.*, 1976).

Chronological differences in vitellogenesis exist between *Loligo bleekeri* and *Todarodes pacificus*. In *L. bleekeri*, as in many other loliginid species, follicle cells occupy most of the volume of the entire oocyte-follicle complex; subsequently, individual follicle cells fuse to form a syncytium, which is engaged in vitellogenesis (Figure 2G). On the other hand, the follicular syncytium in females of *T. pacificus* is formed when follicle cells occupy a relatively small volume of the oocyte-follicle complex and participate in vitellogenesis (TAKAHASHI & YAHATA, 1973; IKEDA *et al.*, 1991). The oocyte-follicle complex of *T. pacificus* approximately corresponds to the one at the early yolkless stage (stage 4, Figure 2E) in *L. bleekeri*. In particular, TAKAHASHI & YAHATA (1973) revealed the existence of a yolk nucleus in oocytes corresponding to ones at the primary growth stage (stage 2, Figure 2C) in *L. bleekeri*. The above-mentioned chronological differences seem to be due to prominent difference in the size of oocytes between the two species. Fundamentally, the oocyte development of *L. bleekeri* is identical to that of *T. pacificus*, except for the vitellogenic process.

The existence of polysaccharid material in the yolk granules of *Loligo bleekeri* is indicated by the vivid PAS reaction seen in Figure 3D. Cytochemical investigations on the composition of yolk in mollusks (*i.e.*, FUJII, 1960; RAVEN, 1961; COWDEN, 1961, 1962, 1968; DONATO CELI, 1967; UBBELS, 1968) have established that yolk granules contain carbohydrates, muco- or glycoproteins, iron-containing proteins, phospholipids, and particular amino acids (tyrosine, tryptophan, arginine).

An analysis of the reproductive cycle of *Loligo bleekeri*

Table 2

The range of TGSI and ML of female *Loligo bleekeri* at the various phases of maturity.

Maturity phase	TGSI (%) (range \pm SD)	ML (mm) (range \pm SD)
I	0.13 (0.02–0.24 \pm 0.08)	92 (68–105 \pm 12)
II	0.37 (0.1–0.71 \pm 0.19)	133 (99–177 \pm 22)
III	0.7 (0.19–1.28 \pm 0.27)	168 (132–222 \pm 19)
IV	2.48 (1.58–4.28 \pm 0.81)	195 (177–223 \pm 16)
V	9.96 (5.16–16.45 \pm 3.12)	249 (209–282 \pm 20)

TGSI: Total gonado-somatic index; ML: Dorsal mantle length.

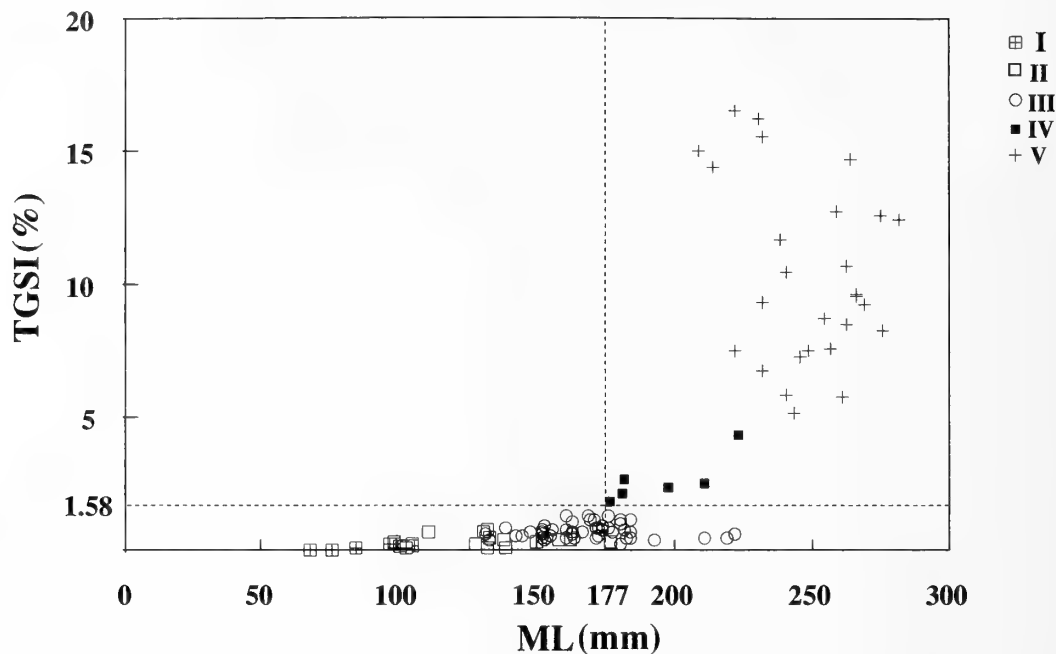


Figure 5

Relation between TGSi and ML of female *Loligo bleekeri* at the various phases of maturity. TGSi: Total Gonadosomatic Index; ML: Dorsal Mantle Length.

demonstrated that active vitellogenesis was completed in a single month. This is an indication of high meiotic rate of oocytes at the vitellogenesis stage. Ovaries of fully mature females are occupied (ca. 75%) mostly by oocytes at the vitellogenesis stage. From the above facts, it may be considered that the oocytes function as recruitment to ripe eggs, which are used in the series of egg-layings. However, it has not been determined whether *L. bleekeri* spawns in series during only one spawning season.

WAKUTSUBO (1989) reported that two different spawning populations coexist on the northern coast of Honshu (Aomori Prefecture). One cohort spawns in winter (winter population, range from December to February) and the other cohort spawns in spring (spring population, range from March to June). Animals used in this study probably belong to the winter-spawning population, based on clear seasonal changes in maturity, ML, and TGSi values. The range of TGSi values of phase V females is extremely wide (5.16–16.45%). This may indicate that egg development is highly asynchronous among individuals and that females of *Loligo bleekeri* are in fact serial spawners. Based on seasonal changes in maturity and ML composition, the life span of *L. bleekeri* is thought to be one year.

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A Comparison of Larval Development, Growth, and Shell Morphology in Three Caribbean *Strombus* Species

by

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Abstract. Development, growth rates, and shell morphology are compared for the larvae of the three most abundant *Strombus* species living in the Bahamas: *S. gigas*, *S. costatus*, and *S. raninus*. Illustrations are provided for positive identifications of the larval shells from field studies. Maximum shell dimensions of *S. costatus*, *S. gigas*, and *S. raninus* differ significantly at hatching ($388 \pm 14 \mu\text{m}$ SL, $354 \pm 15 \mu\text{m}$ SL, and $197 \pm 8 \mu\text{m}$ SL, respectively). The shell length (SL) for these species at competence was correlated with developmental time to competence in laboratory culture ($r^2 = 0.95$). *Strombus raninus* had the largest shell at competence ($1450 \pm 53 \mu\text{m}$ SL) and the longest larval cycle (40 days). *Strombus costatus* was 14% smaller ($1277 \pm 101 \mu\text{m}$ SL) and was competent at 32 days, while *S. gigas* had the smallest shell at competence ($1170 \pm 58 \mu\text{m}$ SL) and the shortest larval period (21 days). These differences in developmental rate suggest species-specific differences in potential larval dispersal and recruitment processes.

INTRODUCTION

In recent years there has been increasing interest in the larval ecology of the queen conch, *Strombus gigas* Linnaeus, 1758. This stems from a need to understand the ecology and recruitment dynamics of this severely overfished Caribbean resource (BERG & OLSEN, 1989; APPELDOORN & RODRIGUEZ, 1992) and an interest in stock rehabilitation through release of hatchery-reared juveniles (BERG, 1976; APPELDOORN & BALLANTINE, 1983; SIDDALL, 1984; DAVIS *et al.*, 1987). Eggs (ROBERTSON, 1959), spawning (RANDALL, 1964), and larval development (D'ASARO, 1965) of *S. gigas* have been described for over 25 years; however, the first reports of distribution and abundance of *S. gigas* veligers were published during the last year (CHAPLIN & SANDT, 1992; STONER *et al.*, 1992a; POSADA & APPELDOORN, 1992).

Seven *Strombus* species inhabit the warm subtropical and tropical waters of the western north Atlantic Ocean, and the biogeography and taxonomic characteristics for adults have been compared (CLENCH & ABBOTT, 1941; ABBOTT, 1974; WALLS, 1980; MOSCATELLI, 1987). In the Bahamas, the three most abundant *Strombus* species are *S. gigas* (queen conch), *S. costatus* Gmelin, 1791 (milk conch), and *S. raninus* Gmelin, 1791 (hawk wing conch),

all of which spawn during the summer (Stoner, personal observations).

The objectives of this study were to compare the larval shell morphologies of *Strombus gigas*, *S. costatus*, and *S. raninus* to assist in positive identifications for field studies, and to compare their development and growth rates in laboratory culture. Differences in growth rates and time to competence are discussed in terms of potential larval dispersal and recruitment processes.

MATERIALS AND METHODS

To compare larval development, *Strombus gigas*, *S. raninus*, and *S. costatus* were cultured at the Caribbean Marine Research Center (CMRC) in Vero Beach, Florida, between May and September 1992, using culture techniques adapted from DAVIS (1992). Culture temperature was 27–30°C, salinity was constant at 35‰, photoperiod was 12L:12D, and seawater was purified with a 10- μm filter and ultraviolet sterilizer.

Newly laid egg masses of *Strombus gigas* and *S. costatus* were collected near the CMRC field station on Lee Stocking Island, Exuma Cays, Bahamas. *Strombus gigas* masses were found on an 18-m deep, coarse-sand breeding site east of the island (STONER & SANDT, 1992). *Strombus*

costatus masses were found on a 2-m deep sandy shoal northwest of the island. Egg masses, collected either the day before or on the morning of shipment, were sent by air to Vero Beach in individual insulated bottles containing about 500 mL of seawater at 26°C. For *S. raninus*, nine mature females and two males were collected in the vicinity of Lee Stocking Island and transported to the CMRC Vero Beach Laboratory. This reproductive stock was maintained in a flow-through downwelling sand tray and fed a variety of macroalgae (primarily *Enteromorpha* sp.). The sand trays were searched daily for egg masses. Portions of two or three egg masses were cultured for each species.

Egg masses were incubated in flow-through upwelling containers. A section of egg mass strand was observed daily under a compound microscope (100 \times) to determine hatch day. Capsulated veligers were ready to hatch when they were observed rotating in their egg capsules; and their velar lobes, eye spots, and orange foot pigments were clearly visible (D'ASARO, 1965; DAVIS, 1992). Within 24 hr of an expected hatch (3–4 days after spawning) several 2–3 cm egg strands were placed in two 1-L beakers (1000 mL seawater/beaker). Approximately 12 hr after emergence, which usually occurred in the early evening, swimming veligers were siphoned into a 73- μ m sieve which was partially submerged in a seawater-filled container to ease larval stress and prevent shell damage. The veligers were rinsed off the sieve and initially stocked in three 1-L beakers (1000 mL seawater/beaker) at a density of 100–200 veligers/L. Culture water was static and aeration was not necessary; however, veligers were transferred into clean water and beakers daily by using a 73- or 200- μ m sieve depending on veliger size. At each water change algal debris and dead veligers were removed with a pipette. Density was gradually reduced by diluting the cultures to 10–20 veligers/L as the veligers neared competence. The veligers were cultured until they were metamorphically competent. Competence was recognized by observing pigmentation changes on the foot (orange to green) (DAVIS, 1992) and swim-crawl behavior (larva uses foot to move on substrate with lobes extended) (Davis, unpublished data).

Larvae were fed Caicos *Isochrysis* cultured with Fritz[®] media in 250-mL Erlenmeyer flasks (GUILLARD, 1975). Feeding began at an initial density of 5000 cells/L and was increased to 7000 cells/L over the culture period. The diet of late-stage veligers was supplemented with 3000 cells/L of *Chaetoceros gracilis* Schutt.

Egg-strand and capsule diameters were measured using a compound microscope with a calibrated ocular micrometer (Figure 1). The number of *Strombus raninus* eggs per egg mass was estimated by separately hatching two egg masses in 10 L of seawater. The hatched veligers were stirred and five 10-mL aliquots were counted. Additional egg-mass data were obtained from ROBERTSON (1959), RANDALL (1964), and DAVIS *et al.* (1984).

Approximately 10 veligers were collected daily from each culture, examined, and then preserved in 5% buffered formalin (95% seawater). Collection began on day one,

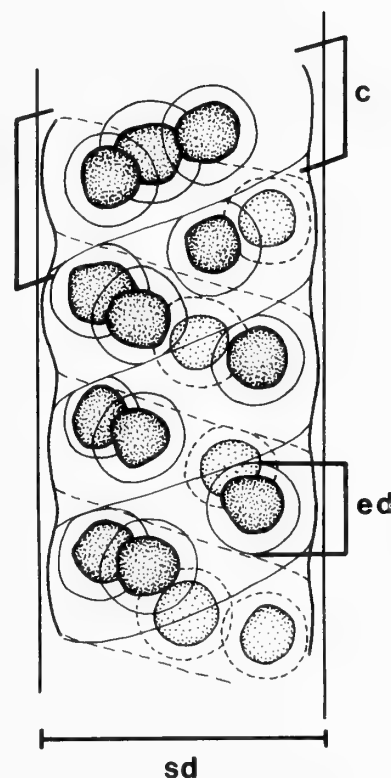


Figure 1

Egg mass strand section: c, coil of the strand; ed, egg capsule diameter; sd, strand diameter.

approximately 12 hr after hatching. Although development of *Strombus* larvae is a continual process, five stages of larval shell development were arbitrarily chosen. These stages were easily recognized and were used for comparisons and illustrations. Stage I represented the newly hatched larva (protoconch I). Stage II larvae were characterized by an elongated beak; for all species this occurred on day 5. Stage III larvae were 530–600 μ m in shell length; they continued to have an elongated beak; and specimens for all three species were collected on day 10. By Stage IV the beaks of all species had diminished to a small point; *S. gigas* and *S. costatus* larvae were collected on day 15 and *S. raninus* larvae on day 20. Stage V larvae were collected when they became competent for metamorphosis as described above (days 21, 32, and 40 for *S. gigas*, *S. costatus*, and *S. raninus*, respectively); at this stage the larval shells had no beak and they had reached their terminal shell size. Maximum shell dimension (MD) was measured for Stage I of each species and also for Stage II of *S. raninus* (Figure 2A). Shell length (SL) was measured for all other stages of each species (Figure 2B). A random sample of 20 shells from Stages I and II, and 10 shells from Stages III, IV, and V were measured using a dissecting microscope (20–40 \times) equipped with an ocular micrometer.

The dorsal and ventral views of the preserved larval shells were projected onto a computer monitor using a

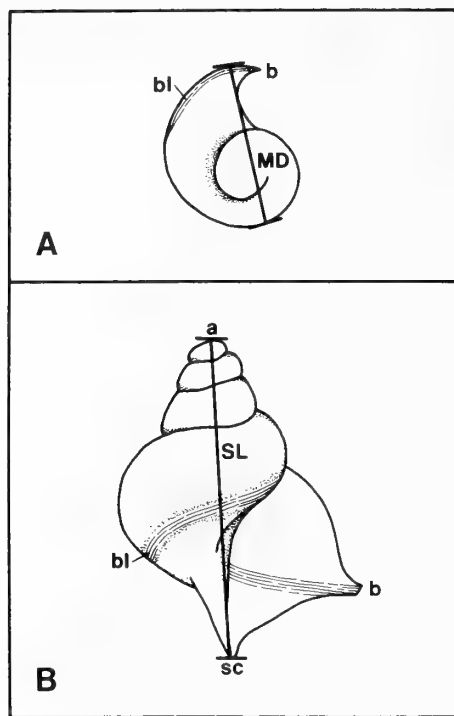


Figure 2

Larval shell measurements. A. Maximum shell dimension (MD). B. Shell length (SL). Terminology: a, apex; b, beak; bl, beak line; sc, siphonal canal.

video camera attached to a dissecting microscope (40 \times). Individual shell images were digitized using a Macintosh video program (MediaGrabber[™]) and transferred to a Macintosh drawing program (Canvas[™]) where an outline

of each shell was drawn to proportion. Shell details seen with the aid of dissecting (40 \times) and compound microscopes (100 \times) were added to the final drawings, which were prepared by a biological illustrator.

RESULTS

Egg Masses

The three *Strombus* species examined lay similar crescent-shaped egg masses, each composed of a single strand of eggs folded back and forth perpendicular to the long axis of the crescent (ROBERTSON, 1959; D'ASARO, 1965). The *S. gigas* egg mass is slightly larger than that of *S. costatus*, but both are larger than the *S. raninus* egg mass (Table 1). Egg-strand diameter shows a similar pattern, wherein the diameter of the egg strand is related to the number of egg capsules per mm of strand length, the number of egg capsules per coil of the strand, and egg-capsule size (Table 1, Figure 1).

The rate at which the eggs develop is temperature dependent (DAVIS & HESSE, 1983; RODRIGUEZ-GIL *et al.*, 1991), and the eggs hatch between 3 and 5 days after spawning at 27–30°C. In this laboratory study, fecundity was calculated for *Strombus raninus*. Nine *S. raninus* females laid 51 egg masses in 46 days (24 July to 7 September), an average of 3.7 egg masses per month per female. *Strombus raninus* females may lay twice as many egg masses per month compared to *S. gigas* females (Table 1).

Larval Development

The newly hatched shells of *Strombus gigas*, *S. raninus*, and *S. costatus* were significantly different in maximum shell dimension (ANOVA, $F_{(2,57)} = 1287$, $P < 0.001$) (Figure 3), and all of the means were significantly different

Table 1

Comparison of egg mass characteristics for three *Strombus* species. Means with one standard deviation and sample number, *n*, in parentheses.

Variables	Species		
	<i>S. gigas</i>	<i>S. raninus</i>	<i>S. costatus</i>
Length of egg mass (cm)	8–15 (9)	4–7 (4)	6–10 (2)
Diameter of egg strand (μ m)	785 \pm 44 (10)	321 \pm 20 (10)	761 \pm 18 (10)
No. eggs/mass	313,000–485,000 (10) ^b	206,000–245,000 (2)	185,000–210,000 (2) ^a
No. egg capsules per mm of strand length	14–16 (10)	21–25 (15)	12–14 (10)
No. eggs per coil of the strand	5–6 ^a	3 ^a	4–5 ^a
Egg capsule diameter (μ m)	225 \pm 17 (20)	140 \pm 4 (30)	262 \pm 6 (20)
Days until hatching at 27–30°C	3–4	3	4
Fecundity (No. egg masses per female per month)	1.7 ^c	3.7	NA

^a ROBERTSON (1959).

^b RANDALL (1964).

^c DAVIS *et al.* (1984).

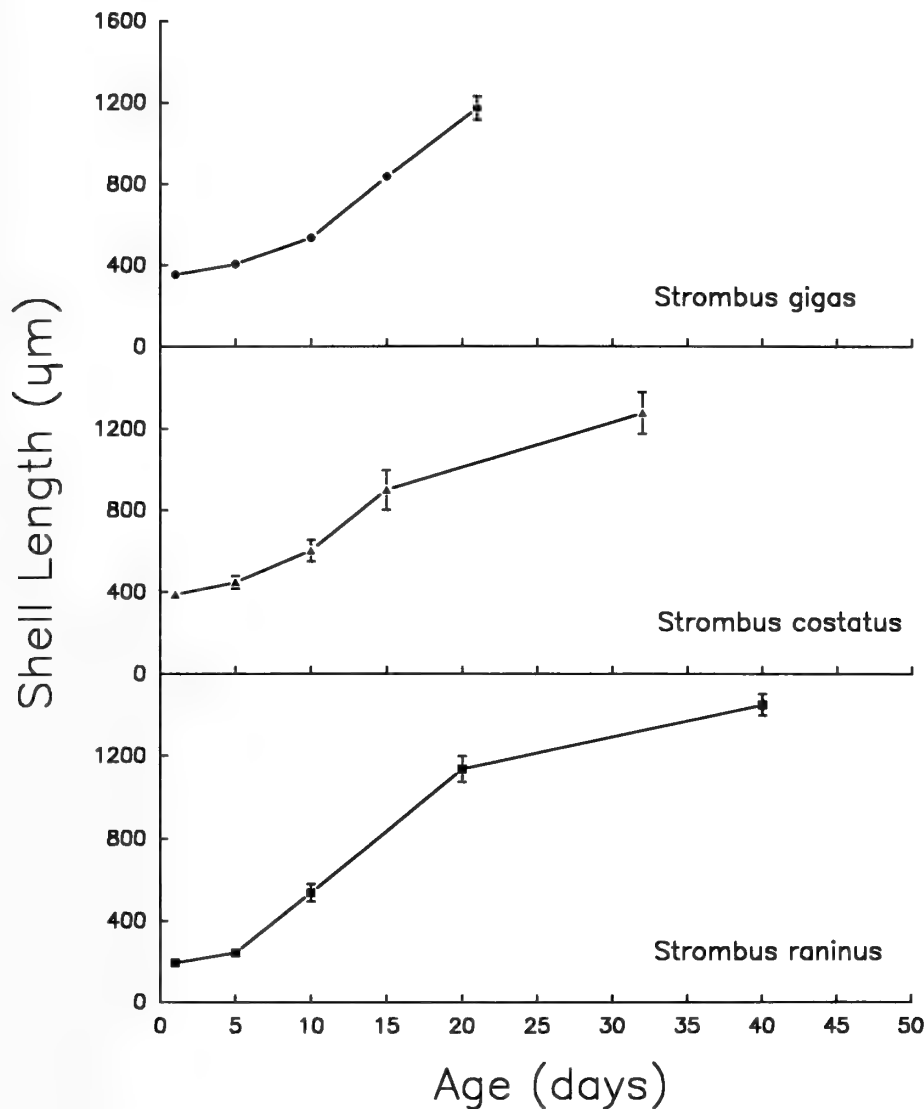


Figure 3

Growth curves for three larval *Strombus* species laboratory cultured at 27–30°C.

(Tukey's multiple comparisons of means, $P < 0.001$). *Strombus costatus* hatched with the largest maximum shell dimension (mean = 388 μm ; SD = 14; $n = 20$), *S. gigas* was 9% smaller (mean = 354 μm ; SD = 15; $n = 20$), and *S. raninus* hatched at approximately half the size of *S. costatus* (mean = 197 μm ; SD = 8, $n = 20$).

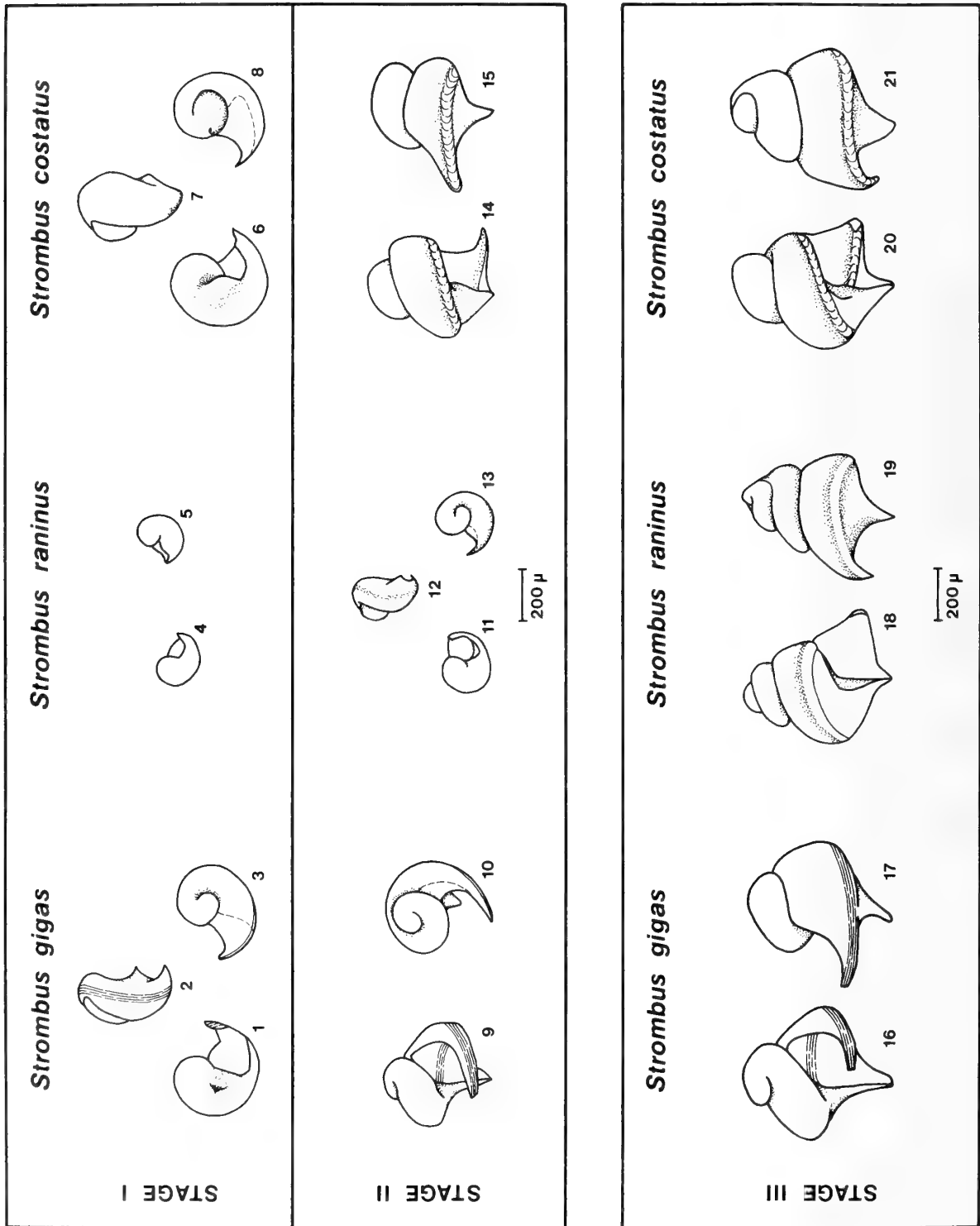
Species differences in shell size at competence were also significantly different (ANOVA, $F_{(2,27)} = 38$, $P < 0.001$) (Figure 3), and all of the means were significantly different (Tukey's multiple comparisons of means, $P < 0.01$). At competence *Strombus raninus* had the longest SL (mean = 1450 μm ; SD = 53; $n = 10$), *S. costatus* was 14% smaller (mean = 1277 μm ; SD = 101; $n = 10$), and *S. gigas* was 24% smaller than *S. raninus* (mean = 1170 μm ; SD = 58; $n = 10$).

Strombus gigas had the fastest growth rate over the entire

larval phase (39 $\mu\text{m}/\text{day}$), and reached competence in the shortest time (day 21) (Figure 3). *Strombus costatus* had an overall growth rate of 28 $\mu\text{m}/\text{day}$, and reached competence in 32 days (Figure 3). *Strombus raninus* had an overall growth rate of 31 $\mu\text{m}/\text{day}$, and reached competence in 40 days (Figure 3). Shell length for these species at competence was correlated ($r^2 = 0.95$) with developmental time to competence (*i.e.*, *S. gigas* larvae were competent at day 21 and had the smallest shell at competence; and *S. raninus* larvae were competent at day 40 and had the largest shell at competence).

Shell Morphology

Larval shell development for *Strombus gigas*, *S. raninus*, and *S. costatus* is illustrated for the five stages described



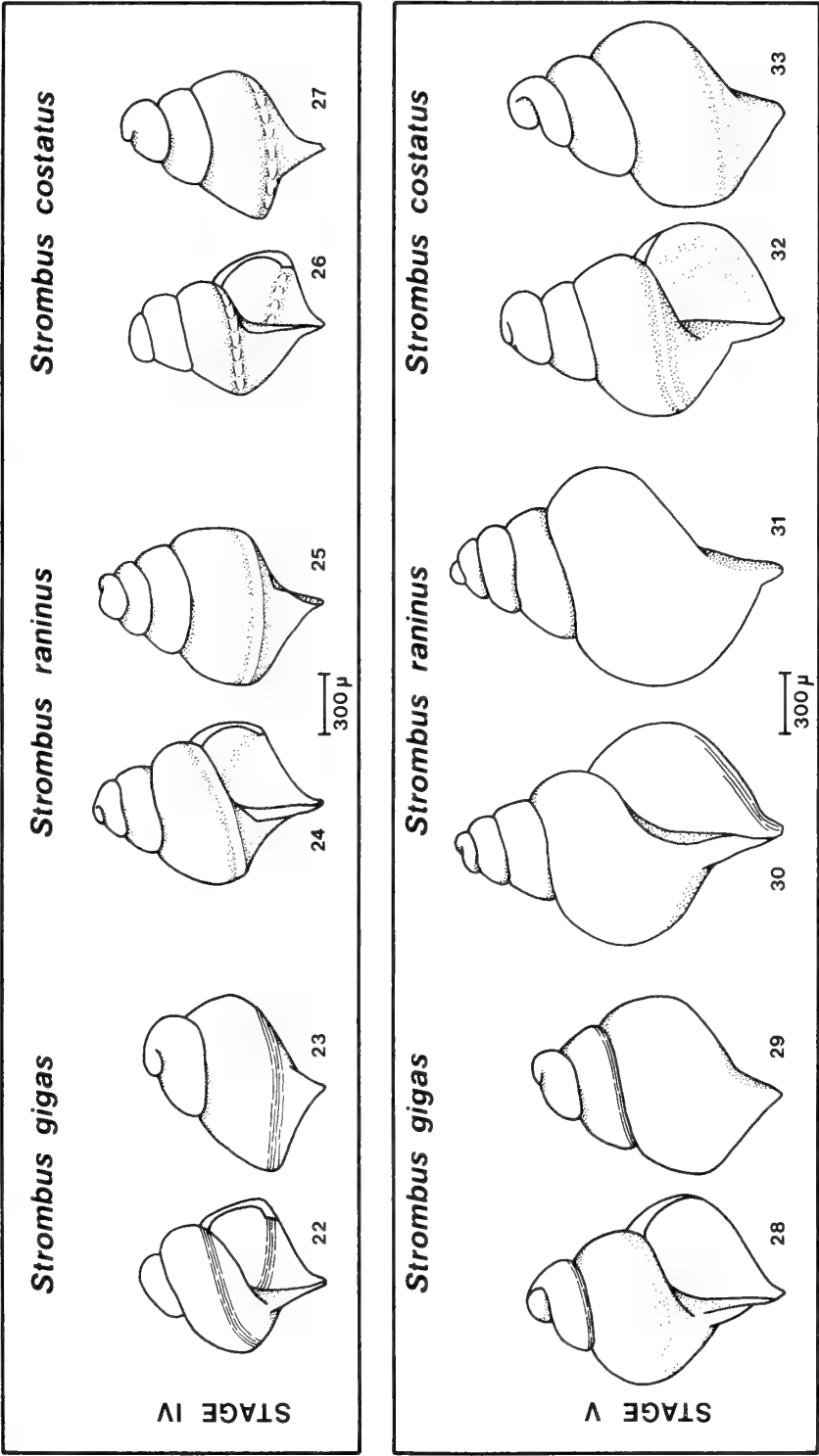


Figure 4
Larval shells of *Strombus gigas*, *S. raninus*, and *S. costatus*. See text (Shell Morphology) for description and comparisons of each stage.

above (Figure 4). Details of beak lines and other markings are best seen by viewing the shells with a dissecting microscope (40–60 \times) and top illumination.

Stages I and II (Figure 4, drawings 1–15): The shells of newly hatched veligers of *Strombus gigas* and *S. costatus* are difficult to distinguish, owing to their similar shape and size. To make accurate identifications, the shell of each species was positioned on edge with the apex and siphonal canal showing (Figure 4, drawings 2 and 7). From this view the SL of *S. costatus* is slightly longer ($\sim 60\ \mu\text{m}$) than that of *S. gigas*. More importantly, the apex of *S. costatus* protrudes like a dome from the beginning of the first whorl. By day 5, *S. costatus* whorls are laid down in a tight spiral, compared to those of the other two species, resulting in a slightly elongated larval shell (Figure 4, drawing 14). Newly hatched and 5-day-old shells of *S. raninus* are approximately 40–50% smaller than the same age larvae of *S. gigas* and *S. costatus*; therefore, they cannot be confused with those of the other two species (Figure 3).

Shell color also distinguishes these three species. At hatching *Strombus gigas* has a creamy, off-white, translucent shell with small pustulate markings, *S. raninus* has a transparent shell with no color, and *S. costatus* has a semi-transparent shell, also with no color. All three species have long beaks; however, the beak lines differ (Figure 2). At hatching *S. gigas* has the most prominent beak line, comprised of four raised parallel lines (striae) which follow the beak whorl (Figure 4, drawing 2). The beak line for *S. raninus* is faint, but resembles a shaded band (Figure 4, drawing 12). *Strombus costatus* also has a faint beak line at hatching, but it becomes more apparent by day 5. This beak line is similar to that of *S. gigas*; however, a repeated C-shaped pattern on the ridge, resembling growth lines, is a more obvious feature (Figure 4, drawings 14 and 15).

At hatching the shells of *Strombus gigas* and *S. costatus* have 1.5 whorls and *S. raninus* has approximately 1.25 whorls. By day 5, *S. gigas* has 2 whorls, *S. raninus* has 1.5 whorls, and *S. costatus* has 2.5 whorls.

Stage III (Figure 4, drawings 16–21): By day 10 the three species are similar in shell length (Figure 3), and the beaks are still elongated; however, the number of whorls differs. *Strombus gigas* has 2.5 whorls, *S. raninus* has 3.5 whorls, and *S. costatus* has 3 whorls. The beak lines on all species are apparent—*S. gigas* with parallel lines (Figure 4, drawings 16 and 17), *S. raninus* with a shaded band which protrudes slightly from the outer whorl (Figure 4, drawing 19), and *S. costatus* with the repeated C-shaped pattern (Figure 4, drawings 20 and 21). The apex of the shell is an important feature for separating the species; in *S. gigas* it is round and blunt (Figure 4, drawing 16), in *S. raninus* small and pointed (Figure 4, drawing 18), and in *S. costatus* dome-shaped and tilted (Figure 4, drawing 20). The shell color of both *S. gigas* and *S. costatus* is now a faint amber. Pustulate markings persist on the *S. gigas* shell through all stages.

Stage IV (Figure 4, drawings 22–27): The shell beak of all three species is less distinct (Figure 4, drawings 22, 24, and 26). Shells have several features distinguishing each other. These include the beak lines (discussed under Stage III), number of whorls (*Strombus gigas* has 3 whorls, *S. raninus* has 4 whorls, and *S. costatus* has 3.5 whorls), shell length (Figure 3), and shape of the shell (*S. gigas* is round and squat [Figure 4, drawings 22 and 23], *S. raninus* is elongated [Figure 4, drawings 24 and 25], and *S. costatus* is elongated with a tilted apex [Figure 4, drawing 26]).

Stage V (Figure 4, drawings 28–33): At competence the beaks of all species have disappeared and only *Strombus gigas* and *S. costatus* have traces of the beak lines remaining (Figure 4, drawings 28, 30, and 32). Sizes differ (Figure 3), and spire shapes are very distinct. *Strombus gigas* has a rounded, squat spire (Figure 4, drawings 28 and 29); *S. raninus* has a triangular, pointed spire (Figure 4, drawings 30 and 31); and *S. costatus* has an elongated spire with slightly concave sides (Figure 4, drawings 32 and 33). The number of whorls at competence also differs: *S. gigas* and *S. costatus* have 4 whorls, and *S. raninus* has 5 whorls. *Strombus costatus* and *S. raninus* shells become more translucent by this stage, and the *S. raninus* shell has small pustulate markings.

Sorting Plankton for *Strombus* Species

Several key characteristics shared by these three *Strombus* species are used to identify them when sorting preserved plankton. Under a dissecting microscope (20–40 \times) the purple-edged, wrinkled velar lobes, creamy white tissue, and black eye spots can be clearly recognized through the shell. Larval shells of these *Strombus* species have a long beak from hatching through day 10, at which time the beak becomes less distinct, vanishing completely by competence. A beak line can be seen on all species, but is most apparent on *S. gigas* shells. All three *Strombus* species hatch with two velar lobes, develop four lobes by day 5, and have six lobes by day 10. The lobes continue to elongate until the veliger becomes competent.

DISCUSSION

Larvae of *Strombus gigas*, *S. costatus*, and *S. raninus* can be clearly distinguished from each other with confidence at all stages. Although our descriptions are based upon laboratory cultures, we have sorted thousands of *Strombus* veligers taken in the Bahamas and Florida with no obvious differences in the morphology between wild and laboratory-reared specimens. Therefore, we believe that the descriptions and illustrations in this study will be applicable in the entire Caribbean region.

Field collections of *Strombus* veligers have been made in the eastern Caribbean Sea (POSADA & APPELDOORN, 1992), the Exuma Cays, Bahamas (CHAPLIN & SANDT, 1992; STONER *et al.*, 1992a, b), and the Florida Keys (Stoner, unpublished data). Most of these collections were made

with 202- μ m-mesh plankton nets towed through approximately 200 m³ in near-surface water. This mesh size appears to be adequate for efficient collection of newly hatched *S. gigas* and *S. costatus* veligers, but surveys for smaller strombid veligers, such as those of *S. raninus*, will require a mesh size not exceeding 150 μ m. This smaller mesh would increase considerably the time necessary for sorting. Densities as high as 2.0 *S. gigas* veligers/m³ are known in areas around the Exuma Cays where reproductive stocks are high (Stoner, unpublished data). Tows made in the Exuma Cays during high wind periods frequently result in zero *S. gigas* and *S. costatus* veligers recovered, even during peak larval season (Stoner, unpublished data). This may be related to sinking of veligers during periods of high turbulence; therefore, sampling during rough conditions should be avoided.

Collections should be preserved in a buffered (pH = 7.5–8.5) formalin-seawater mixture. The shells of newly hatched strombids are thin and important identification features (*i.e.*, beaks, beak lines, and siphonal canals) are subject to relatively rapid loss by dissolution in acidic solutions. The heavier shells of late stage larvae are considerably more durable and easily preserved. With reasonable attention to preservation, even early stage *Strombus* veligers have been stored for periods exceeding two years without significant dissolution.

Larval Dispersal Processes

From routine laboratory and hatchery cultures of *Strombus gigas* and *S. costatus* larvae, growth rates and time to competence are known to vary with temperature, nutrition, and density of culture (BOIDRON-METAIRON, 1992; BROWNELL, 1977; DAVIS, 1992; GLAZER & BERG, 1992; M. Gongora, personal communication; L. Rodriguez-Gil, personal communication). For instance, the onset of competence for *S. gigas* larvae can occur between 16 and 28 days, and *S. costatus* larvae can become competent as soon as 20 days and as late as 35 days. *Strombus raninus* larvae have not been cultured routinely; however, variations in the number of days to competence occurred in this study. Some larvae showed signs of competence at 38 days and others as late as 48 days, but the mean numbers of days to competence was 40.

Our examination of larval development under uniform culture conditions permits a comparison of water-column mortality and long-distance dispersal in the three subject species. *Strombus gigas* should have the lowest water-column mortality because of its rapid development and short larval life. On the other hand, the high fecundity of *S. raninus* may be an adaptation to long larval life and associated high mortality rates during the planktonic phase. Widespread gene flow among Caribbean populations of *S. gigas* (MITTON *et al.*, 1989; CAMPTON *et al.*, 1992) could be related to the length of larval life and larval transport processes. In a typical Caribbean surface current of 0.2–0.5 m/sec (GRANT & WYATT, 1980; KINDER, 1983), an

S. gigas veliger could be transported 43 km per day or about 900 km during the three-week larval period. *Strombus costatus* would be transported approximately 1400 km, and *S. raninus* approximately 1800 km, twice the distance of *S. gigas*. With these calculations, populations of *S. gigas* in the Florida Keys could have originated in spawning sites in Mexico or Cuba but could probably not have a source farther south or east in the Caribbean Sea. *Strombus raninus* larvae, however, could be transported across most distances in the Caribbean region. Precise knowledge of transport potential will depend upon new information on variations in developmental rates for wild larvae exposed to changes in nutrition, temperature, and salinity during their planktonic period, and on the ontogenic behavior of the veligers, particularly that related to vertical migration.

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Studies on the Reproduction and Gonadal Parasites of *Fissurella pulchra* (Gastropoda: Prosobranchia)

by

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Abstract. Reproduction in the keyhole limpet *Fissurella pulchra* was studied at Huayquique, northern Chile, and the parasitism of its gonad by the digenean trematode *Proctoeces humboldti* was analyzed. The reproductive condition was assessed through the gonadosomatic index (GSI). Mean GSI showed two marked declines during the study period (in late autumn and in summer), suggesting the occurrence of two spawning periods per year. The *F. pulchra* population under study seems to be a partial spawning one, where the various size classes spawn at different seasons. Full reproductive potential seems to be attained at about 55 mm in shell length; thus, harvesting of individuals shorter than 60 mm (6 cm) in shell length for commercial or industrial purposes is not advisable. The prevalence and mean intensity of infection by *Proctoeces* increase with the size of the limpet hosts. The prevalence of infection did not differ between females and males, nor did the percentages of infection vary among monthly samples through the collecting period.

INTRODUCTION

The largest keyhole limpets of the genus *Fissurella* live on Chilean coasts. During the past 15 years, these gastropod mollusks have progressively attracted research workers' attention, particularly after Bretos reported the presence of adult digenean trematodes parasitizing the gonads of *Fissurella* (BRETOS & JIRÓN, 1980). This finding suggests that these mollusks are the definitive hosts for trematodes of the genus *Proctoeces*.

Fissurella pulchra Sowerby, 1835, is a rare species of the genus. It is restricted to certain habitats, where its populations seem to have low density. Biological studies on it are limited to taxonomy (McLEAN, 1984), biometry, habitat and epibiotic organisms fixed on the shell (BRETOS & CHIHUAILAF, 1990), and the finding that trematodes occur in 77.5% of the specimens analyzed in northern Chile (BRETOS & JIRÓN, 1980). *Fissurella pulchra* can be found from Salaverry, Peru (8°14'S) to Río Bio-Bio, Concepción Province, Chile (36°48'S) (McLEAN, 1984). McLean detected only small individuals at most Peruvian localities; the largest were living in central Chile.

In spite of the scarce knowledge of *Fissurella pulchra*, it has been exploited as food, together with other limpets in Chile (BRETOS, 1988), at Coquimbo, Iquique, San An-

tonio, and Talcahuano. Consequently, it is important to study such basic aspects of its life cycle as reproduction and growth.

The aim of this paper is to present aspects of the reproduction and occurrence of the trematode *Proctoeces humboldti* George-Nascimento & Quiroga, 1983, in the gonads of *Fissurella pulchra* in northern Chile.

MATERIALS AND METHODS

Random samples of *Fissurella pulchra* were taken at Huayquique (20°17'S, 70°8'W) every two months from April 1979 to May 1980. Collections were made from rocky substrates by diving in shallow waters, from 1.5 to 3 m below the low-water mark. Sampling covered the available size range.

Shell length was measured to 0.1 mm, and body and gonad wet weight to 0.1 g. The sex of each limpet was determined by dissection. The hypothesis of equal representation of both sexes in the *Fissurella pulchra* population under study was tested. Chi-square was calculated by using the correction for continuity of Yates (ZAR, 1984). The trematodes found in the ovary and testes were counted.

Length data were grouped in size classes of 5 mm each. The reproductive condition for each individual was eval-

Table 1

Examined material of *Fissurella pulchra* from Huayquique. *n* = number of females or males; % = percentage of sexes; M = percentage of animals estimated as ripe; Und = sexually undetermined specimens.

Date	Sexed animals						Und	Total
	Females			Males				
	<i>n</i>	%	M	<i>n</i>	%	M		
Apr. '79	37	60.6	44.4	24	39.4	91.7	1	62
Jun. '79	19	47.5	0	21	52.5	5.0	0	40
Sep. '79	16	33.3	28.6	32	66.7	60.0	1	49
Nov. '79	24	48.9	75.0	25	51.1	92.0	0	49
Jan. '80	27	58.6	46.2	19	41.4	66.7	3	49
Mar. '80	15	30.0	0	35	70.0	17.1	2	52
May '80	24	55.8	17.4	19	44.2	44.4	4	47
Total	162			175			11	348

uated on the basis of a gonadosomatic index (GSI), and on the gonadal characteristics. GSI was calculated by expressing the ratio of gonad weight to the total soft-part weight as a percentage. Monthly GSI means were calculated for each sex. Sexual maturity of each animal was estimated by considering its GSI and the size and appearance of the gonad (BRETOS *et al.*, 1983). A table with minimum GSI values per size class was made, to classify each animal as sexually mature if it had a GSI equal to or higher than minimal GSI. The minimum GSI was arbitrarily calculated by adding a one to the mean GSI in each size class divided by two, using samples where most of the animals collected presented high GSI values.

The prevalence and intensity of infection by trematodes were analyzed in sexed *Fissurella pulchra* of all sizes classes. Statistical tests applied to this analysis were performed following the methodology recommended by ZAR (1984), and the significance level of $\alpha = 0.05$ was chosen. Parasitologic terms used are those recognized by MARGOLIS *et al.* (1982).

Surface seawater temperature was recorded at 08:30 hr (minimum temperature) in the sampling site during the study period, and monthly mean values were calculated.

RESULTS

Among the 348 *Fissurella pulchra* individuals collected, 162 were females, 175 were males, and 11 were juveniles of undetermined sex (Table 1). The population of *F. pulchra* was not large enough to allow collection of larger and more frequent samples.

Females measured from 26.8 to 64.7 mm in shell length, males from 27.5 to 63.5 mm, and juveniles from 24.8 mm to 53.3 mm. Mean size in females was 47.48 mm (SD \pm 8.43 mm) in shell length and 48.52 mm (SD \pm 7.32 mm) in males in the whole sample of *Fissurella pulchra*. There was no significant difference between these mean values

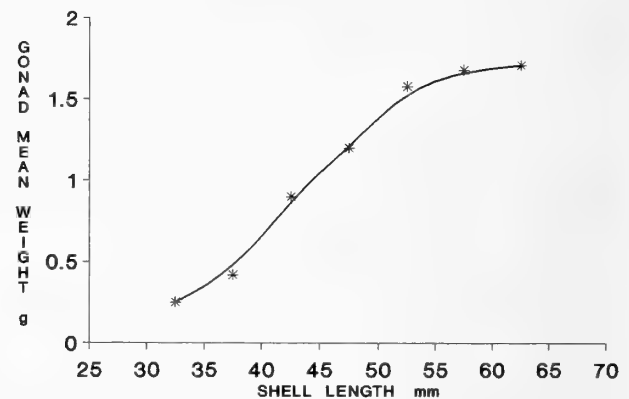


Figure 1

Mean values of gonad wet weight per size class in *Fissurella pulchra* from Huayquique.

(Student's test, $t = 0.976$; $P = 0.329$). As was shown by variance analysis, mean shell lengths in monthly samples were significantly different ($F = 6.063$; $P < 0.001$).

Sexes and Gonads

Fissurella pulchra has separate sexes. No signs of hermaphroditism or sex change were detected at any shell length.

Sex cannot be discerned from external features in these keyhole limpets, only from direct examination of the unpaired gonad. Sexually undetermined juveniles have a small or undetectable gonad, which is translucent or whitish in color. Ovaries are green, and testes are pale yellow, varying to beige. Morphological characters of the gonads in *Fissurella pulchra* are similar to those previously described for *F. maxima* (BRETOS *et al.*, 1983).

The mean weight of gonads in the whole sample (Figure 1) increased until the 50–55 mm shell length size group. No significant growth occurred over this size. The mature ovary attained a wet weight of 4.0 g, and the mature testes 3.1 g in the population under study.

Sex Ratios

Of the sexed animals, 48.1% were females and 51.9% were males, giving a sex ratio of 1:1 in the population examined ($\chi^2 = 0.427$; $P = 0.513$).

The proportions of sexes in specimens of all lengths are constant (Figure 2), supporting the conclusion that sex reversal is absent in the species. Some significantly different sex ratios were observed in some months (Table 1). Males were more numerous in September and March, while females predominated in April, January, and May.

Reproductive Condition

A GSI value was used to assess the reproductive activity of each limpet. The assumption is that an increase in GSI

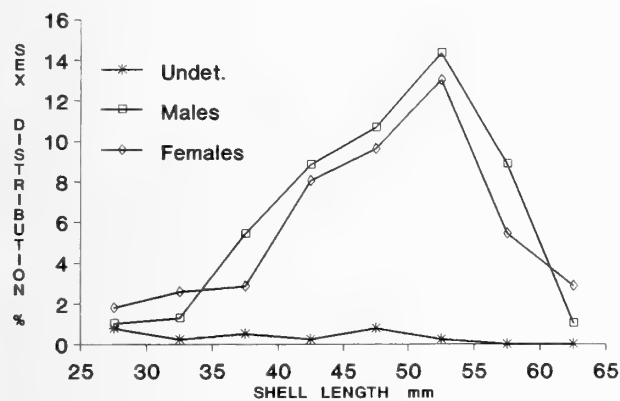


Figure 2

Percentages of sexes per size class in *Fissurella pulchra* collected at Huayquique.

correlates with a build-up of gametogenic cells, while a decrease indicates spawning.

Mainly on the basis of its GSI, each animal was classified as "ripe" or "spent." Limpets with spent and recovering gonads were classed together as spent individuals; specimens with high GSI values were considered as sexually mature or ripe. Table 1 shows the sexual maturity estimates for both sexes in each sample. Many females were mature in April, November, and January, while mature males were also numerous in September. Mature males were present in all samples examined.

The smallest female estimated as sexually mature was 30.1 mm in shell length, and the smallest male measured 30.2 mm. However, the minimum size at which sexual maturity is attained by the studied population could not be determined, because insufficient quantities of specimens were in each analyzed sample. Many individuals of *Fissurella pulchra* classified as sexually mature (Table 1) occurred in April and in November. No mature females were detected in June or in March, and mature males also were scarce in these months.

Monthly mean GSI values varied throughout the year (Figure 3). GSI variations in both sexes followed the same tendency, although the mean GSI in males always showed higher values than those in females.

The relationship between GSI and size in samples with the highest GSI values (Figure 4) shows that GSI increases as the animal grows until 55 mm in shell length; over this size GSI declines.

Spawning

The lowest values of monthly mean GSI (Figure 3) were found in June 1979 and in March 1980, meaning that animals had spent gonads at these dates. The estimates of sexual maturity (Table 1) showed a sharp decrease in the same samples. These findings suggest that the *Fissurella pulchra* population has finished a reproductive period in June and in March. Spawning probably occurred in May–

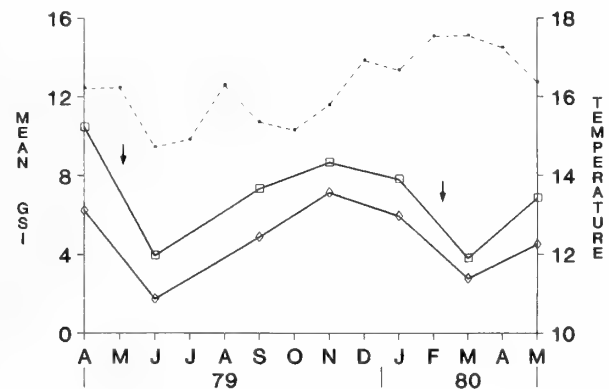


Figure 3

Variations in mean gonadosomatic index per sample in *Fissurella pulchra*, and mean minimal temperatures of the surface seawater at Huayquique. Squares: GSI of males; diamonds: GSI of females. Arrows show presumable spawning periods.

June (late autumn) and between December and February (summer).

A decrease in seawater temperatures coincides with the spawning period of late autumn (arrow in Figure 3), and the highest temperatures of the year coincide with the summer spawning period. These facts seem to support a relationship between fluctuations in seawater temperature and gamete release.

The detection of more than one spawning period per year could have been due to different age classes (size classes) releasing their gametes at different seasons. For this reason, mean GSI per size class was analyzed for each sample. Horizontal lines (Figure 5) were drawn to mark the minimum GSI to be considered as ripe in each class. The oldest animals collected (over 60 mm in shell length) were ripe in January (Figure 5e), spawning probably in summer. The youngest specimens (30–40 mm) seemed to spawn in spring (Figure 5c, d, e). The median size classes

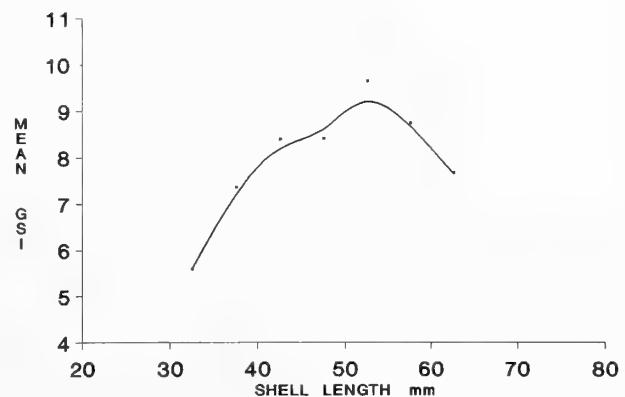


Figure 4

Mean gonadosomatic index for size class of *Fissurella pulchra* collected in April and November ($n = 109$) at Huayquique.

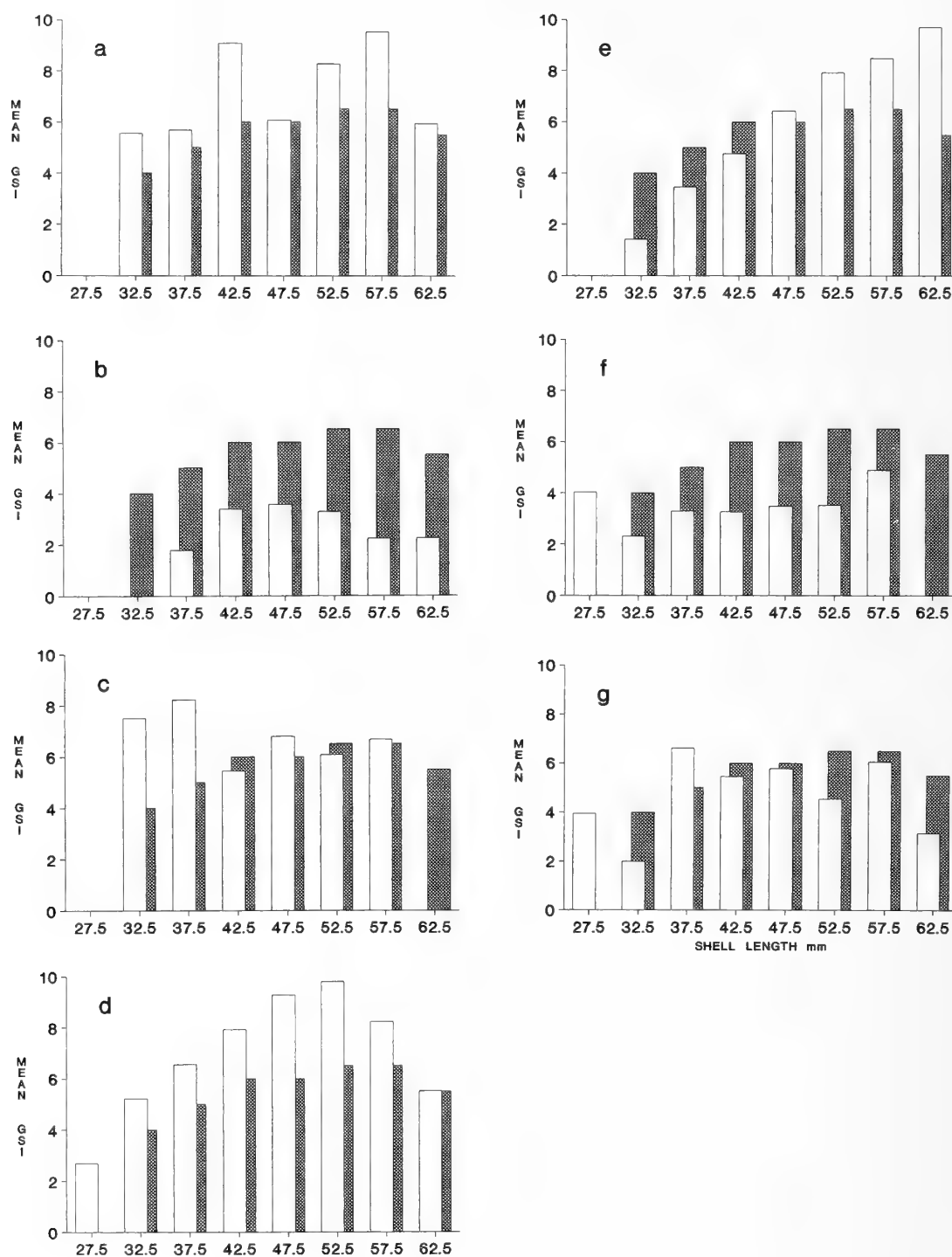


Figure 5

Mean gonadosomatic index (GSI) per size class of *Fissurella pulchra* in each monthly sample (empty bars) and minimal GSI to be estimated sexually mature in each size group (black bars). a. April 1979. b. June 1979. c. September 1979. d. November 1979. e. January 1980. f. March 1980. g. May 1980.

appeared to spawn in late autumn (Figure 5a, b) and late spring (Figure 5d, e).

Parasites in the Gonads

The prevalence of infection by *Protoeces humboldti* was 83.38% among the sexed *Fissurella pulchra* examined, 85.5% among females and 81.1% among males. There were no significant differences between the prevalence in the two sexes ($G = 0.003$; $P = 0.316$). Only two sexually undetermined specimens were parasitized, one of them had one trematode and the other had three.

The prevalence of infection (using angular transformation) in size classes increased with increasing shell length (Figure 6; $r = 0.89$; $P > 0.02$; $n = 8$). All limpets over 55 mm in shell length were parasitized. There was a high exponential correlation between the mean intensity of infection and the size of *Fissurella pulchra* ($r = 0.934$; $P < 0.001$; $n = 8$) (Figure 6).

The prevalence of infection, evaluated using a contingency table, showed little variation throughout the year, and there were no significant differences among the percentages of infection of monthly samples ($\chi^2 = 0.89$; $P = 0.96$). Variations in the prevalence of infection through the seasons had no correlation to mean size per sample ($r = 0.01$; $P = 0.92$; $n = 7$).

The smallest infected female was 26.8 mm long, while the smallest infected male was 27.5 mm long. The mean intensity of infection in sexed animals was 5.92 ± 5.23 trematodes per keyhole limpet host. Infection intensity in females ranged from 1 to 42 (in a 62.1 mm female) parasites per host (mean 6.54 ± 5.98), and it fluctuated in males from 1 to 22 (in a 58.1 mm male) (mean 5.38 ± 4.30). Mann-Whitney tests revealed no significant differences ($Z = 1.59$; $P > 0.05$) in mean intensity for the two sexes.

The mean intensity of infection displayed small fluctuations during the study period. Peaks in mean intensity were observed in September, January, and May, while the lowest values occurred in November and March. Variations in mean intensity through the seasons were correlated to mean size per sample ($r = 0.681$; $P = 0.09$; $n = 7$).

DISCUSSION

In *Fissurella* species, sex can be determined for individuals of sizes 26–28 mm (BRETOS *et al.*, 1983, 1988a). In spite of this, sexually undetermined individuals have been detected over 53 mm in *F. pulchra* and *F. picta*, and up to 72 mm in *F. maxima*. In the last species it was assumed that gonad development was retarded by the high prevalence (73.7%) of trematodes found in juvenile gonads, which presented an intensity of infection ranging up to 17 parasites per host (BRETOS *et al.*, 1983). Only a few individuals of undetermined sex were found in collected samples of *F. picta* and *F. pulchra*, and they were sparsely parasitized. This fact suggests that in the analyzed populations of these

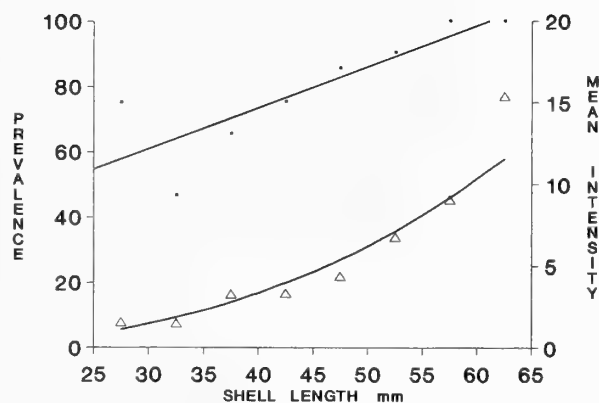


Figure 6

Prevalence of infection (black squares) and mean intensity (open triangles) per size class in *Fissurella pulchra*.

last two species, gonadal development may be mainly determined by individual variability and other endogenous factors.

Although hermaphroditism or change of sex has been mentioned for *Fissurella* (BACCI, 1947) or for *Haliotis* (GIRARD, 1972), these phenomena have not been observed in Chilean fissurellids (BRETOS *et al.*, 1983, 1988a, b; OSORIO *et al.*, 1986). The sex ratio is 1:1 in *F. pulchra* from Huayquique, the same as in *F. nigra* (BRETOS *et al.*, 1988b), in *F. picta* (BRETOS *et al.*, 1988a), and in *F. maxima* from Huayquique (BRETOS *et al.*, 1983) and from Los Vilos (OSORIO *et al.*, 1986). Occasionally, an archaeogastropod may show a disparity of sexes, as has been observed in *F. barbadensis*, a small-sized Caribbean species (WARD, 1966) or in some *Haliotis* species (SHEPHERD & LAWS, 1974).

In *Fissurella pulchra* the mean GSI increases until 55 mm in shell length (Figure 4), diminishing at greater sizes. The same tendency has been shown to occur in the abalone *Haliotis midae* (NEWMAN, 1967), in a relationship between gonad bulk index (equivalent to GSI) and size. This seems to indicate that the gonads attain their maximum development (*i.e.*, their full reproductive potential), at sizes around 55 mm in *F. pulchra*. Longer individuals have reduced reproductive potential. Based on these considerations, it appears not advisable to catch *F. pulchra* specimens shorter than 60 mm in shell length for commercial or industrial purposes.

The *Fissurella pulchra* population under study seems to demonstrate partial spawning, where the various size classes spawn at different seasons, but the population as a whole shows two main spawning periods per year (Figure 3). These periods are explained by the release of gametes of median and large-sized animals. The spawning of small individuals (up to 40 mm) seems to be of low intensity, and does not have significance to the population.

Reproductive data are available for some other Chilean *Fissurella* species. Variations in GSI suggest that *F. maxima*

presents two spawning periods per year: the main in late spring-early summer, and a secondary period in winter, at Huayquique, northern Chile (BRETOS *et al.*, 1983). Studies conducted at Queule and Cheuque, in southern Chile, have shown a similar spawning pattern for *F. nigra* (in late summer, and winter) (BRETOS *et al.*, 1988b) and for *F. picta* (in late summer, and in spring) (BRETOS *et al.*, 1988a). In all these species, animals considered to be ripe were present throughout the year, although they were scarce or absent in some months.

Fissurella barbadensis from the coasts of Barbados presents two principal spawning periods (WARD, 1966): from September to November and from March to June. Histological analysis also showed spawning specimens in all except two samples. These findings agree with those obtained for Chilean keyhole limpets. Partial spawning has not been investigated in those species.

Concholepas concholepas, a Chilean gastropod, also presents more than one spawning period per year at Caleta Hornos (29°38'S, 71°20'W) according to variations observed in the population mean GSI (LOZADA *et al.*, 1989). The highest GSI values occurred in January and in April-May, where all size groups were spawning (70-110 mm). Nevertheless, different reproductive behavior was detected among widely different size groups.

The prevalence of trematodes in the gonads of *Fissurella* species is highly variable, from 13.97% in *F. crassa* to 96.97% in *F. maxima* (BRETOS & JIRÓN, 1980). The prevalence of *Proctoeces humboldti* was nearly constant in *F. pulchra* during the study period. The same has been observed in *Batillus cornutus* infected by *P. ichiharai* (SHIMURA, 1980), or in *Nucella lapillus* by *P. maculatus* (PONDICK, 1983). These findings could be related to a long adult life-span of the parasite, as in the case of *P. ichiharai* (SHIMURA, 1980). No seasonal influence on the prevalence of infection by *Proctoeces* in *F. maxima* from Los Vilos (OSORIO *et al.*, 1986) or in *F. crassa* from Antofagasta (OLIVA & DÍAZ, 1988) has been demonstrated.

The prevalence of infection by *Proctoeces* is influenced by the host's locality. Different prevalences have been detected in *Fissurella crassa* from Iquique (13.97%) (BRETOS & JIRÓN, 1980) or Antofagasta (80.4%) (OLIVA & DÍAZ, 1988). A similar occurrence was reported by PONDICK (1983), in which the intertidal snail *Nucella lapillus* from two sites of the same beach presented different percentages (0% and 4.7%) of infection by *P. maculatus*. The dissimilar prevalences of the same parasite in the same hosts could be attributed to the diverse ecological conditions in the habitats (microhabitats) occupied by these gastropods at those geographical places.

The prevalence of infection by *Proctoeces humboldti* increases with the size of the host in *Fissurella pulchra* (this study) and in *F. crassa* from Antofagasta (OLIVA & DÍAZ, 1988). In *F. maxima* from Los Vilos (OSORIO *et al.*, 1986) prevalence reaches its highest values in median-sized individuals, decreases in larger animals, and is absent in the oldest specimens. OSORIO *et al.* (1986) assumed that the

lower prevalence presented by large-sized limpets was due to their living in deeper habitats, removed from infecting larvae.

The relationship between mean intensity of infection and the size of hosts varies from one species to another. Data reported for *Fissurella maxima* from Los Vilos suggest that there is no relation between these two variables. In *F. crassa* from Antofagasta, intensity is directly correlated to host length, while in *F. pulchra*, we have found an exponential relationship between mean intensity of infection and the shell length of the hosts.

Although OLIVA & DÍAZ (1988) stated that there are significant differences in the mean intensity of infection according to host sex, we have not detected differences between females and males.

Further studies on *Proctoeces humboldti* will be needed to understand its relations with *Fissurella* species. Among these are the elucidation of the life cycle and life-span of this parasite, and the identification of the conditions required for infecting the keyhole limpets.

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Genital Dimorphism in the Land Snail *Chondrina avenacea*: Frequency of Aphally in Natural Populations and Morph-specific Allocation to Reproductive Organs

by

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Abstract. Several species of simultaneously hermaphroditic land snails show a genital dimorphism: aphillic individuals differ from euphallic ones by a lack of male copulatory organs (penis and genital retractor muscle). Aphillic individuals can self-fertilize or outcross as females but not as males. Thus, the mating system of a population may be significantly influenced by the proportion of aphillic individuals.

We present data on the frequency of aphally in 21 natural populations of the rock-dwelling land snail *Chondrina avenacea* in the surroundings of Basel, Switzerland. The populations varied greatly in percentage of aphillic individuals, ranging from 0.9 to 89.2% (grand mean 41.2%). This variation did not follow any discernible geographical pattern. The proportion of aphillic snails within a population was influenced neither by local population density nor by any other habitat characteristics (exposure of rock face, altitude of locality, number of other snail species present).

The populations varied significantly in adult shell size. Within populations, aphillic individuals tended to be smaller than euphallic ones. After controlling for size differences, the reproductive organs amounted to 28.3% of the total body mass in aphillic snails and to 31.7% in euphallic snails in a population. This difference can be explained by the absence/presence of male copulatory organs, whose dry weight was 3.2% of the total body mass of euphallic individuals. Monthly sampling of snails from one population revealed that individuals of *Chondrina avenacea* did not change their sex type over the course of one year.

INTRODUCTION

Different reproductive systems have evolved in hermaphrodites that allow different individuals within a population to reproduce either by self-fertilization or by outcrossing (*e.g.*, gynodioecy in plants; GOUYON & COUVET, 1987). Aphally may be a comparable feature in hermaphroditic snails. Whereas the reproductive structure of snails usually consists of one hermaphrodite gonad and of male and female ducts with accessory glands (= euphallic snails), aphillic individuals lack the male copulatory organs (TOMPA, 1984). Aphillic snails can self-fertilize or outcross as female, but not as male, whereas euphallic individuals can outcross and self-fertilize (POKRYSZKO, 1987, 1990). Thus, the mating system of a population may be

significantly influenced by the ratio of aphillic to euphallic individuals.

Aphally has been reported from numerous species of freshwater and terrestrial gastropods (WATSON, 1923; TOMPA, 1984; POKRYSZKO, 1987) and has received most attention in the freshwater snail *Bulinus truncatus* (*contortus*) (Audouin) (LARAMBERGUE, 1939; JARNE & DELAY, 1991; JARNE *et al.*, 1992; SCHRAG *et al.*, 1992). Pure aphillic, pure euphallic, and mixed populations occur in this species. In the rock-dwelling land snail *Chondrina clienta* (Westerlund), the frequency of aphally varied from 52.2 to 99.1% in 23 natural populations on the Baltic island of Öland, Sweden (BAUR *et al.*, 1993). Breeding experiments have revealed that both genetic and nongenetic components may influence the proportion of aphillic offspring in a

population. (LARAMBERGUE, 1939; SCHRAG *et al.*, 1992; BAUR *et al.*, 1993). Recently, SCHRAG & READ (1992) provided experimental evidence for a temperature-sensitive phally determination during the egg and hatchling stage in two populations of *Bulinus truncatus*.

Sex allocation theory predicts that aphillic snails can invest more in gametes than euphallic ones because they have no cost related to the building and maintenance of male organs, if one assumes that both types of snails invest the same amount of energy in growth and survival (HEATH, 1977; CHARNOV, 1982). This prediction presupposes that aphillic individuals do not adjust their female reproductive organs (albumen gland, female duct) to increase egg production.

This paper examines aphillic and sex allocation in the rock-dwelling land snail *Chondrina avenacea* (Bruguière) in the surroundings of Basel (Switzerland). In particular, the following questions were addressed: (1) how frequently do aphillic individuals occur in natural populations of *C. avenacea*? (2) Is the frequency of aphillic associated with any habitat characteristics, local population density and/or snail size? (3) Do aphillic individuals have reduced fixed costs to build-up their reproductive organs compared with euphallic ones? And (4) is there any seasonal variation in the frequency of aphillic individuals within a population (*i.e.*, do individuals of *C. avenacea* change their sex type over the course of a year)?

MATERIALS AND METHODS

Species

Chondrina avenacea occurs on rock faces and walls in limestone areas of western Europe and the Alps, attaining altitudes of 2000 m (KERNEY & CAMERON, 1979; GITTENBERGER, 1984). *Chondrina avenacea* has determinate growth; its cylindro-conical shell is dextral and in adults is 6 to 8 mm high (GITTENBERGER, 1973; NEUCKEL, 1981). In northwestern Switzerland, *C. avenacea* co-occurs with *Clausilia parvula* Férussac and *Pyramidula rupestris* (Draparnaud) on calcareous rock faces. *Chondrina avenacea* is very resistant to drought (NEUCKEL, 1981). The snails' specialized radula enables them to graze epi- and endolithic lichens growing on rock faces (SCHMID, 1929; BREURE & GITTENBERGER, 1982; BAUR *et al.*, 1992). The snails are active during periods of high air humidity. During winter (November–March) they are active only under mild conditions (warm rains); otherwise, they hibernate in small fissures or attached to the exposed rock surface (NEUCKEL, 1981; BAUR & BAUR, 1991). Dispersal of marked *C. avenacea* on a rock wall (population 16; see below) averaged 234 cm in three months, the maximum distance recorded being 746 cm (B. Baur & A. Baur, unpublished data). Little is known concerning the life history of *C. avenacea*. Preliminary results indicate that individuals complete their shell growth at an age of 3–5 years. Adult snails live 2–10 years (B. Baur, unpublished data).

Sampling

Specimens of *Chondrina avenacea* were collected on vertical rock walls ranging in height from 2 to 60 m in the surroundings of Basel, northwestern Switzerland (47°30'N, 7°40'E), between July and October 1991. Samples consisting on average of 101 (range 65–117) fully grown *C. avenacea* were collected from areas of 4.5–24 m² (mean = 10.9 m²) at each of 20 localities (for convenience referred to as populations) (Figure 1). Localities were situated at least 750 m apart from each other (in most cases several kilometers). At an additional locality (population 21: an isolated, 7 m long and 2–4 m high rock wall), samples consisting of 21–28 snails (mean = 22.8) were collected at monthly intervals from April 1991 to March 1992.

At each locality the following variables were recorded: altitude (in meters above sea level), exposure of the rock face (degrees from south), number of other snail species present on the same face, area to which sampling was restricted (in m²), and local population density of *Chondrina avenacea*. Snail density was estimated by counting the number of adults picked up with a pair of tweezers within 3 min by one of us (BB). Density estimates were based on 3–4 replicates (mean = 3.2) at each locality. A second estimate of local population density was obtained by relating the number of snails collected within 3 min to the sampling area (number of snails per 3 min and m²).

Measurements

The snails were frozen at –20°C. The size (total shell height) of each individual was measured to the nearest 1/24 mm using a binocular microscope with a stage micrometer (a previous study revealed that most of the interpopulational variation in shell size of *Chondrina clienta* can be expressed by the single character of shell height (BAUR, 1988)). The animals were dissected to determine their genital morph (aphillic or euphallic). Both sex types are illustrated by GITTENBERGER (1973).

To evaluate differences in allocation to reproductive organs in aphillic and euphallic individuals and any seasonal changes in the allocation pattern, the genitals of snails from population 21 were separated from the soft body under a dissecting microscope. In euphallic individuals, the male copulatory organs (penis, epiphallus, penis retractor muscle) were also separated from the remaining parts of the reproductive organs (albumen gland, spermoviduct, female duct). The dry weight of the soft body, male copulatory organs (if present) and remaining genitals were determined (after drying for 48 hr at 100°C) using a Mettler AE163 balance (accuracy 0.01 mg).

Statistical Analysis

Data analysis was performed using the SAS program package (SAS INSTITUTE INC., 1989). Among-population differences in the proportion of aphillic snails were evaluated using chi-squared tests. Correlation analysis was

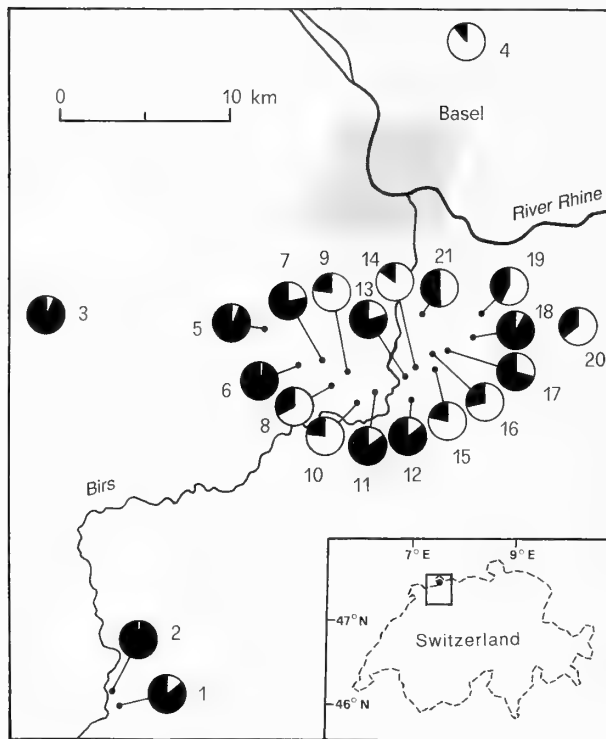


Figure 1

Frequencies of aphillic and euphallic individuals in natural populations of *Chondrina avenacea* in the surroundings of Basel, Switzerland. Open sections refer to aphillic individuals and solid sections to euphallic individuals. Sample size for each population is given in Table 1. Stippled area indicates the city of Basel.

used to examine any possible association between frequency of aphillic snails and local population density and altitude of the locality. Frequency data were arcsine-transformed. Possible influences of the exposure of rock faces and the number of co-existing snail species on the percentage of aphillic *Chondrina avenacea* were evaluated by analysis of variance (ANOVA). Students *t*-tests were used to examine differences in body mass and reproductive organs between aphillic and euphallic individuals.

RESULTS

Variation in Aphally Among Populations

The populations varied greatly in the frequency of aphillic individuals, but this variation did not follow any general geographical pattern (Figure 1). On average 41.2% of the snails were aphillic; the among-population variation ranged from 0.9 to 89.2% (Table 1). In most cases, populations situated 750 m from each other differed significantly in the percentage of aphillic individuals. However, there were two groups, each of three neighbor populations, in which the three populations did not differ in the proportion of aphillic individuals (populations 8, 9, and 10: $\chi^2 = 3.08$, $df = 2$, $P > 0.2$; populations 11, 12, and 13:

$\chi^2 = 1.23$, $df = 2$, $P > 0.4$; Table 1, Figure 1). These neighbor populations were also isolated from each other; for example, populations 11 and 12 were separated by a distance of 2.1 km with a 170-m deep valley and a 20-m wide river between them.

Local population density varied from 13.7 to 70.7 adults collected in 3 min or from 0.7 to 17.7 individuals collected per m^2 in 3 min (Table 1). However, the proportion of aphillic snails within a population was not correlated with local population density (number of snails collected in 3 min: $r = 0.17$, $n = 21$, $P = 0.47$; number of snails/ m^2 and 3 min: $r = 0.29$, $n = 21$, $P = 0.20$). Furthermore, the proportion of aphillic snails was not correlated with the altitude of the locality ($r = -0.24$, $n = 21$, $P = 0.29$). Populations of *Chondrina avenacea* inhabit E-, S-, and W-exposed rock faces (Table 1). The exposure of the habitat had no significant effect on the proportion of aphillic individuals (one-way ANOVA, $F = 0.66$, $df = 5$, $P = 0.66$). The number of other snail species co-occurring with *C. avenacea* ranged from 0 to 5 (Table 1), but had no significant effect on the proportion of aphillic individuals in *C. avenacea* (one-way ANOVA, $F = 1.84$, $df = 5$, $P = 0.17$). Furthermore, the presence/absence of *Clausilia parvula* and *Pyramidula rupestris* (which occurred at 16 [76.2%] and 12 [57.1%] of the 21 localities examined) had no effect on the proportion of aphillic individuals in *Chondrina avenacea* (presence/absence of *Clausilia parvula*: $t = 0.89$, $df = 19$, $P = 0.38$; *P. rupestris*: $t = 0.12$, $df = 19$, $P = 0.91$).

The populations varied significantly in adult shell size (Table 1). In general, aphillic snails were slightly smaller than euphallic ones (two-way ANOVA: population effect, $F = 46.92$, $df = 20$, $P < 0.0001$; sex type, $F = 4.57$, $df = 1$, $P = 0.033$; interaction, $F = 1.65$, $df = 20$, $P = 0.034$). The difference in shell height averaged 0.06 mm, which corresponds to 0.95% of the mean shell height or approximately to 2% of the total wet weight. Considering single populations, this difference was significant in only three of 21 populations (population 10: $t = 3.76$, $n = 108$, $P < 0.001$; population 14: $t = 2.71$, $n = 90$, $P < 0.01$; population 21: $t = 4.05$, $n = 251$, $P < 0.001$).

Mean shell size of *Chondrina avenacea* tended to decrease with local population density ($r = -0.38$, $n = 21$, $P = 0.09$), which may indicate intraspecific competition. In contrast, mean shell size of *C. avenacea* was positively correlated with the number of other snail species present on the rock faces (Spearman rank correlation $r_s = 0.65$, $n = 21$, $P = 0.0014$), suggesting that some localities are more suitable for snails than other localities. Mean shell size was neither correlated with the altitude of the locality ($r = 0.19$, $n = 21$, $P = 0.42$) nor affected by the exposure of the rock face (one-way ANOVA, $F = 2.17$, $df = 5$, $P = 0.11$).

Allocation to Reproductive Structures

Aphillic individuals from population 21 were significantly smaller (shell height) and slightly lighter (soft body

Table 1

Percentage of apthallic individuals in natural populations of *Chondrina avenacea* in the surroundings of Basel (northwestern Switzerland), with local population density, shell size of fully grown snails, and habitat characteristics.

Locality ^a	% apthallic snails	<i>n</i>	Population density ^b $\bar{x} \pm \text{SE}$	Shell height (mm) $\bar{x} \pm \text{SE}$	Altitude (m)	Exposure	Other species ^c
1	14.0	114	54.7 \pm 5.6	5.98 \pm 0.03	720	S	0
2	0.9	109	43.0 \pm 2.7	6.37 \pm 0.03	550	SW	1
3	6.4	110	31.0 \pm 2.7	6.29 \pm 0.03	600	S	1
4	89.2	74	18.0 \pm 2.5	6.25 \pm 0.03	400	E	1
5	6.2	112	30.3 \pm 3.4	6.41 \pm 0.03	410	SW	5
6	1.5	65	17.7 \pm 1.3	6.80 \pm 0.05	590	NE	5
7	21.3	108	32.3 \pm 0.3	6.56 \pm 0.03	500	W	2
8	67.6	102	34.7 \pm 1.2	6.20 \pm 0.03	590	W	1
9	77.4	84	21.3 \pm 3.9	6.43 \pm 0.04	440	SW	3
10	76.9	108	35.7 \pm 0.9	6.42 \pm 0.03	610	E	2
11	14.9	101	33.3 \pm 2.4	5.87 \pm 0.03	500	S	1
12	14.4	104	22.8 \pm 3.5	7.06 \pm 0.03	580	W	3
13	19.8	91	30.0 \pm 2.9	6.49 \pm 0.04	460	S	2
14	84.8	92	20.0 \pm 3.0	6.39 \pm 0.04	440	SW	2
15	78.4	116	49.3 \pm 3.9	6.17 \pm 0.03	610	S	2
16	70.3	118	70.7 \pm 4.1	6.45 \pm 0.03	510	W	2
17	43.1	102	19.5 \pm 4.5	6.74 \pm 0.03	720	SW	1
18	8.2	85	13.7 \pm 3.4	6.88 \pm 0.04	650	E	4
19	57.3	117	49.0 \pm 2.1	6.71 \pm 0.03	630	SE	3
20	64.1	103	46.7 \pm 3.2	6.26 \pm 0.03	510	S	2
21	49.5	273	59.7 \pm 2.9	6.45 \pm 0.02	490	W	2

^a For location of sites see Figure 1.

^b Number of fully grown snails collected within 3 min.

^c Other species included: family Cyclophoridae: *Cochlostoma septemspirale* (Razoumowsky); family Pyramidulidae: *Pyramidula rupestris* (Draparnaud); family Orculidae: *Orcula dolium* (Draparnaud); family Chondrinidae: *Abida secale* (Draparnaud); family Enidae: *Ena montana* (Draparnaud); family Clausiliidae: *Cochlodina laminata* (Montagu), *Clausilia parvula* Férussac, *Macrogastra plicatula* (Draparnaud), *Lacinaria plicata* (Draparnaud); family Helicidae: *Helicigona lapicida* (Linné).

dry weight) than euphallic snails (Table 2). However, differences in soft body mass disappeared after differences in shell were controlled for ($t = 0.33$, $df = 22$, $P = 0.74$). Irrespective of size, individuals of both sex types differed in allocation to reproductive structures, which averaged 28.3% of the total body mass in apthallic snails and 31.7% in euphallic snails (Table 2). The male copulatory organs of euphallic snails amounted to 3.2% of the total soft body weight (or to 9.9% of the reproductive structures), which corresponds approximately to the difference in allocation to reproductive structure measured between the two sex types (3.4%; Table 2).

Seasonal Changes in Weight of Reproductive Structures

Figure 2 shows the percentage of apthallic individuals collected from population 21 at monthly intervals between April 1991 and March 1992. The frequency of apthallic snails did not change significantly in the course of one year ($\chi^2 = 10.67$, $df = 11$, $P > 0.4$). This indicates that individuals of *Chondrina avenacea* did not change their sex type.

Figure 3 shows the seasonal variation in the relative weight of the reproductive structures for apthallic and eu-

phallic *Chondrina avenacea*. The reproductive structures of euphallic snails were throughout the year heavier than those of apthallic snails.

DISCUSSION

Variation in Aphally Among Populations

Our study demonstrated a large variation among populations in the percentage of apthallic individuals. The range of variation (0.9–89.2%) exceeds that found in natural populations of *Chondrina clienta* on the Baltic island of Öland, Sweden (52.2–99.1%; BAUR *et al.*, 1993). Comparing both studies, apthallic individuals appear to occur more frequently in *C. clienta* (grand mean: 77.7%) than in *C. avenacea* (grand mean: 41.2%). This suggests that *C. avenacea* might on average have a higher outcrossing rate than *C. clienta*.

The degree of allozyme variation is often considered as an indicator of the type of breeding system employed (*e.g.*, SELANDER & OCHMAN, 1983; BROWN & RICHARDSON, 1988). Enzyme electrophoresis revealed that all individuals in the samples from five populations of *Chondrina clienta* on Öland were homozygous and allelically identical at each of the 17 putative loci assayed (BAUR & KLEMM, 1989).

Table 2

Shell height and dry weight of soft body and reproductive structures of aphillic and euphallic *Chondrina avenacea* from population 21. Mean values based on 12 monthly samples are presented.

Variable	Aphillic snails ($\bar{x} \pm SE$)	Euphallic snails ($\bar{x} \pm SE$)	t-value	P
Shell height (mm)	6.38 \pm 0.02	6.53 \pm 0.03	4.59	<0.001
Soft body dry weight (mg)	1.411 \pm 0.037	1.496 \pm 0.038	1.58	0.127
Reproductive organs				
dry weight (mg)	0.401 \pm 0.018	0.476 \pm 0.025	2.41	0.025
% soft body	28.3 \pm 0.8	31.7 \pm 1.1	2.38	0.026
Male copulatory organs				
dry weight (mg)	—	0.047 \pm 0.003	—	—
% soft body	—	3.2 \pm 0.2	—	—

The lack of heterozygosity in *C. clienta* suggests that self-fertilization is the prevailing breeding system. Corresponding data are not available for *C. avenacea*.

As in *Chondrina clienta*, the variation in genital dimorphism in populations of *C. avenacea* did not follow any discernible geographic pattern, nor was it associated with any particular habitat characteristic. Genital dimorphism in *C. avenacea* might be adapted to fine-grained, so far unknown ecological conditions of the snails' habitat. We found no intermediate stage in which the penis was only partly developed; it was always either present or absent. In population 21, the proportion of aphillic *C. avenacea* remained constant in monthly samples over one year. Similarly, POKRYSZKO (1987) found no seasonal changes in the percentage of aphillic individuals in a population of *Vertigo pusilla* Müller in Poland. All evidence so far available indicates that individuals become either euphallic or aphillic during ontogeny and that, later at the adult stage, they are unable to resorb or build up male copulatory organs (LARAMBERGUE, 1939; POKRYSZKO, 1987, 1990; BAUR *et al.*, 1993).

We found no correlation between the proportion of aphillic snails and local population density. This suggests that the frequency of aphilly is not a simple function of

the mate encounter rate. Breeding experiments revealed that both genetic and nongenetic components may influence the proportion of aphillic offspring in the freshwater snail *Bulinus truncatus* (LARAMBERGUE, 1939; SCHRAG *et al.*, 1992). SCHRAG & READ (1992) found that the temperature experienced during the egg and hatching stage affected phally determination in two populations of *B. truncatus*. Little is known concerning the determination of genital dimorphism in land snails. POKRYSZKO (1990) reported that one euphallic and two aphillic individuals of *Vertigo pusilla* did not differ in the proportion of aphillic and euphallic offspring produced by selfing. BAUR *et al.* (1993) raised juveniles of *Chondrina clienta* in the laboratory to examine whether different conditions of food supply and population density experienced during ontogeny affect the expression of genital dimorphism. Snails from one population become euphallic more frequently under conditions of low food supply than expected under complete genetic determination. This suggests that, in addition to a genetic

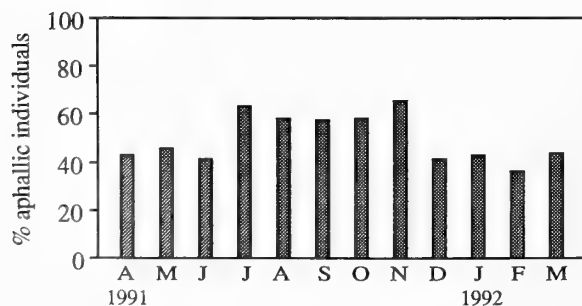


Figure 2

Seasonal variation in percentage of aphillic *Chondrina avenacea* collected at monthly intervals from population 21.

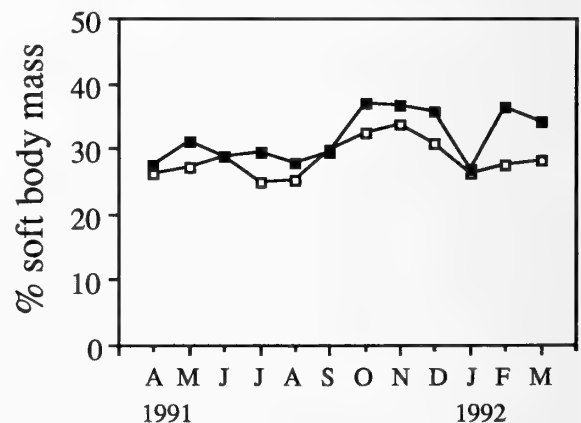


Figure 3

Seasonal variation in dry weight of reproductive structures of (□) aphillic and (■) euphallic *Chondrina avenacea* collected at monthly intervals from population 21.

component, the expression of the genital dimorphism can be influenced by environmental conditions. However, detailed breeding experiments are needed to elucidate the mechanism of the determination of genital dimorphism in land snails.

Mean shell size of *Chondrina avenacea* tended to decrease with local population density, indicating intraspecific competition. Similarly, shell size of *C. clienta* was negatively correlated with local population density on the Baltic island of Öland (BAUR, 1988). Experiments demonstrated that intraspecific competition affects juvenile growth rate, age at maturity, adult shell size, and survival of *C. clienta* (BAUR & BAUR, 1990). The observed competitive interactions appeared to be a result of both exploitation and interference by mucus trails (BAUR & BAUR, 1990).

Allocation to Reproductive Structures

Simultaneous hermaphroditism is assumed to be advantageous in animals of low mobility and in animals that live in low-density populations, for it decreases the risks of fitness loss as a result of lack of mating partners (TOMLINSON, 1966; GHISELIN, 1969; CHARNOV, 1982). Hermaphroditism also offers opportunities for self-fertilization. However, hermaphroditism carries increased fixed costs because each parent must build and maintain two sets of reproductive apparatus. A hermaphrodite therefore has less resources to invest in gametes and would be expected to produce fewer eggs and sperm than gonochoristic equivalents (HEATH, 1977). The fixed costs of hermaphroditism can be reduced by organ sharing in the reproductive system (HEATH, 1977). For example, the gonad (hermaphroditic gland) of pulmonate snails has a shared structure for producing both eggs and sperm. Aphally may be another way to reduce fixed costs for hermaphroditic snails with frequent or obligate selfing. Due to the reduced fixed costs for the reproductive structures, aphyallic snails might have more energy for growth and reproduction (JARNE & DELAY, 1991). Indeed, aphyallic individuals of *Bulinus truncatus* (a species with indeterminate growth) were larger and produced more eggs than euphallic snails of the same age (JARNE *et al.*, 1992). In contrast, our results indicate that aphyallic *Chondrina avenacea* were smaller and invested less energy into reproductive structures than euphallic individuals. In *C. clienta*, the male reproductive structures develop during the subadult stage; the sex type could be assessed in individuals larger than 4.7 mm (BAUR *et al.*, 1993). However, the genitals were not fully developed before shell growth had been completed. Thus, the sex type appears to be determined before the final adult size is attained. Nonetheless, aphyallic individuals of *C. avenacea* may invest less resources in growth and reproductive structures than euphallic ones. Consequently, one would expect that aphyallic snails have an enhanced reproductive output. Experiments are needed to test this hypothesis.

The present study demonstrated a great variation in the

proportion of aphyallic individuals in natural populations of *Chondrina avenacea*. This indicates that the rates of outcrossing and self-fertilization may vary among populations. However, the selective forces that shape the prevailing mating patterns are still unknown.

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A New Species of *Otostoma* (Gastropoda: Neritidae) from Near the Cretaceous/Tertiary Boundary at Dip Creek, Lake Nacimiento, California

by

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Abstract. A neritid gastropod *Otostoma aethes* Squires & Saul, sp. nov., from uppermost Cretaceous or possibly lowermost Paleocene strata on the south side of Lake Nacimiento, San Luis Obispo County, California, is the only confirmed occurrence of this genus from the Pacific coast of North America. The presence of this Tethyan genus is suggestive of a warm K/T boundary climate.

INTRODUCTION

A new species of a large-sized neritid gastropod is described from a locality in marine strata in the Dip Creek area, northern San Luis Obispo County, central California (Figure 1). The strata are important because they were deposited near the Cretaceous-Tertiary boundary and perhaps include the boundary. Gastropods, as well as bivalves, of this age are poorly known on the Pacific coast of North America, and more than half of the species remain undescribed (SAUL, 1986).

The Dip Creek fauna contains some mollusks that resemble genera or species usually considered to indicate a Paleocene age, as well as some indicative of a Cretaceous age. TALIAFERRO (1944) did not construe the mixture of ages to indicate closeness to the Cretaceous-Tertiary boundary but apparently interpreted the mixture as a result of redeposition of Cretaceous rocks within Paleocene sediments. Within these sediments, however, there is not a segregation of "Cretaceous forms" from "Paleocene forms" (SAUL, 1986). In the Dip Creek area, turritellas dominate the fauna. MERRIAM (1941) named and described the most common species as *Turritella pachecoensis adalaidana*, and TALIAFERRO (1944) assigned a Paleocene

age to the enclosing rocks. SAUL (1983) restudied the turritellas and assigned the Dip Creek species to *T. peninsularis adalaidana* Merriam, 1941, and *T. webbi* Saul, 1983. She inferred a latest Maastrichtian and possibly an earliest Paleocene age for the strata there.

At Dip Creek, the turritellas and other mollusks are shallow-water forms that have undergone post-mortem transport and are within deep-water turbidites in beds of coarse-grained grit or conglomerate (GROVE, 1986). TALIAFERRO (1944) referred the Dip Creek strata to his Dip Creek Formation, but he was not aware of the sedimentologic and stratigraphic complexities in the area. DURHAM (1968) mapped the outcrops along the north shore of Lake Nacimiento as unnamed Upper Cretaceous and lower Tertiary rocks, and GROVE (1986) used this designation for the outcrops along the south shore of the lake. Confident assignment of the Dip Creek section to a formation can be done only after much-needed detailed geologic mapping in the Lake Nacimiento/Dip Creek area is undertaken (V. M. Seiders, personal communication).

TALIAFERRO (1944:516) listed only 12 taxa from the Dip Creek Formation, and at least three of these [*Amaurellina* sp., *Tornatellaea pinguis* (Gabb, 1864), and *Turritella infragranulata* Gabb, 1864] were undoubtedly from

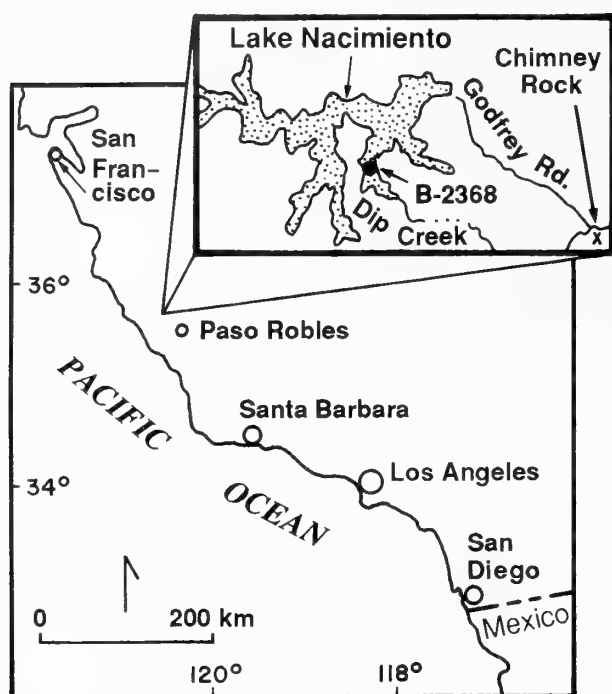


Figure 1

Location map for UCMP loc. B-2368, Lake Nacimiento area, San Luis Obispo County, California. (After SAUL, 1986:fig. 1).

outcrops northwest of Chimney Rock along Godfrey Road. These rocks were excluded from Taliaferro's Dip Creek Formation and Durham's unnamed Upper Cretaceous and lower Tertiary rocks by HOWELL *et al.* (1977), who recognized them as a flysch sequence conformably overlying the unnamed Upper Cretaceous and Tertiary rocks, but with a probable hiatus between. DURHAM (1968) provided a list of mollusks from near the base of this flysch sequence indicative of a late early Paleocene age (about zone P3) (SAUL, 1983, 1986). Of the remaining nine taxa listed by TALIAFERRO (1944), the three purported *Turritella* species are all *T. peninsularis adelaidana*, and this subspecies is by far the most abundant taxon present. The only other species that can be considered to be of common occurrence is *Venericardia (Pacifcor) taliaferroi* Verástegui, 1953. Neither *Calva (Calva) baptisia* Saul & Popenoe, 1992, nor *Turritella webbi* Saul, 1983, is common. SAUL (1986) listed or figured 10 or more undescribed species, and most of these are represented by one or two specimens. If the composition of this fauna from very near the K/T boundary is to be recorded, the descriptions will apparently have to be based, in most cases, on very few specimens.

A single specimen of *Otostoma aethes* sp. nov. was found by N. L. Taliaferro in 1943(?) at University of California Museum of Paleontology (Berkeley) [= UCMP] loc. B-2368, along the south shore of Lake Nacimiento, at the east side of Dip Creek near the base of a canyon wall, 120°55'40"N, 35°43'45"W, NE ¼ NE ¼ of section 30,

T25S, R10E, U.S. Geological Survey, 7.5-minute, Lime Mountain, California, quadrangle, 1948 (photorevised 1979), San Luis Obispo County, central California. The specimen was enclosed in hard, coarse-grained sandstone that required considerable effort by the junior author to remove.

The outcrops in Dip Creek are usually covered by waters behind the Lake Nacimiento dam but are exposed during drought years. In 1977, 1985, and 1986, the junior author visited the vicinity of UCMP loc. B-2368 but was unable to find any more specimens of the new species. We are reluctant to name a new species based on a single specimen, but the likelihood of finding more specimens is remote.

SYSTEMATIC PALEONTOLOGY

Family NERITIDAE Rafinesque, 1815

Subfamily NERITINAE Rafinesque, 1815

Genus *Otostoma* d'Archiac, 1859

Desmieria DOUVILLÉ, 1904:344-346. COSSMANN, 1925:199-203.

Type species: *Nerita rugosa* Hoeninghaus, 1830, *non* Gmelin, 1791; = *Natica rugosa* Goldfuss, 1844, *non* Bosc, 1801; = *Natica subrugosa* d'Orbigny, 1850 (new name) [= *Nerita rugosa* Roemer, 1841; ? = *Otostoma ponticum* d'Archiac, 1859], by indication DOUVILLÉ (1904:346).

Discussion: *Otostoma* has a globose shell, with a low spire, rapidly expanding whorls, and collabral ornamentation. Some species have some subordinate spiral sculpture, especially about the base, that tends to be broken into nodes by the collabral ribs. The deck is broad and reduces the apertural opening. The inner lip has several large teeth that extend onto the roundly callused deck. The collabral sculpture and roundly callused deck readily distinguish typical *Otostoma* from *Nerita* Linné, 1758.

D'ARCHIAC (1859) listed five species in his new genus: *Otostoma tchihatcheffi* d'Archiac, *O. ponticum* d'Archiac, *O. rugosum* d'Archiac, *O. pouechi* d'Archiac, and *O. valenciennesi* d'Archiac, but chose no type species. Although all are listed as though d'Archiac were the author, for *O. rugosum* d'Archiac, he provided a synonymy consisting of "*Natica rugosa*, Hoeninghaus, Goldfuss, p. 119, pl. 199, fig. 11a, b (a poor picture), *N. subrugosa*, d'Orbigny, Prodrome, p. 221." Additionally he mentioned that some of the specimens examined by him are from the upper part of the "craie de Maastricht." He excluded, because the figure is too poor, *Nerita rugosa* ROEMER (1841:83, no. 1, pl. 12, fig. 6), which D'ORBIGNY (1850) had included in his replacement name *Natica subrugosa*.

DOUVILLÉ (1904) proposed the name *Desmieria* as a replacement name for *Otostoma* d'Archiac because of the supposed conflict with *Otostomus* Beck, 1837, and designated as type of *Desmieria* the best known species "*Desm.*

rugosa, de la craie de Maastricht," Netherlands. The type species of *Desmiera* is therefore, by original designation, one of the species d'Archiac included in *Otostoma*. Douvillé thus set the type species of *Otostoma* by indication because fixing the type species of either the original or the replacement name fixes the type species of the other (RIDE *et al.*, 1985, article 67). That Douvillé referred to the type species only as *Desmiera rugosa* does not prevent its recognition as the *Otostoma rugosum* listed by d'Archiac, because both Douvillé and d'Archiac referred to its occurrence in the craie de Maastricht. KEEN & COX (1960) indicated that *Natica rugosa* Roemer, 1841, is the type species by subsequent designation of COSSMANN (1925:199), although Cossmann actually presented *Nerita rugosa* Hoeningh. as the type species of *Desmiera*, probably following Douvillé's indication, which is earlier and adequate.

Several authors, including DARTEVELLE & BREBION (1956), GLIBERT (1962), and WENZ (1938), have listed the type species of *Otostoma* as *O. ponticum* d'Archiac. The source of this may be FISCHER (1887:800), who listed *O. ponticum* d'Archiac in parentheses. Although FISCHER (1880–1887) in many cases explicitly indicated type species in parentheses, he also did the same for examples. In the case of *Otostoma* he failed to indicate whether *O. ponticum* should be considered the type species or only an example, and he cannot be considered to have designated the type.

The first usage that we have found of the specific name *rugosa* for the *Otostoma* from the "craie de Maastricht" is that of HOENINGHAUS (1830:467) in the combination *Nerita rugosa*. *Natica rugosa* has also been used (ROEMER, 1841; HOENINGHAUS in GOLDFUSS, 1844). Both combinations are junior primary homonyms; for the former, *Nerita rugosa* Gmelin, 1791, has priority and for the latter, *Natica rugosa* Bosc, 1801, for both of which D'ORBIGNY (1850) provided *Natica subrugosa* d'Orbigny, 1850.

DOUVILLÉ (1904) also recognized that there are three different groups among D'ARCHIAC's (1859) five species of *Otostoma*. The first three, *O. tchihatcheffi*, *O. ponticum*, and *O. rugosum*, and *Otostoma*; *O. pouechi* is a *Corsania*; and *O. valenciennesi* may be a *Velates* Montfort, 1810.

Otostoma aethes Squires & Saul, sp. nov.

(Figures 2–4)

Diagnosis: An *Otostoma* with prominent shoulder on body whorl, a few low spiral ribs on anterior third of body whorl, noded at intersections by low collabral ribs; deck broad and rather flat with seven subequal teeth along inner lip margin.

Description: Shell thick, medium sized, height 30 mm, width 27.3 mm. Body whorl rapidly expanding with subangulate shoulder. Spire very low, apex elevated slightly above flattened dorsal surface. Sculpture of several low collabral swellings, most prominent aperturally, strongly prosocline, and fairly prominent on dorsal area near outer lip; anterior third of body whorl with three very low

spiral ribs, faintly noded at intersection with collabral swellings; posteriormost spiral obsolete aperturally.

Aperture large, somewhat quadrate, anterior end trough-shaped. Outer lip sturdy, beveled anteriorly. Deck broad, much reducing aperture, with seven teeth along slightly curved inner lip margin; anteriormost two teeth small, next two strongest, next two moderately strong, and posteriormost one small. Four strongest teeth extend onto deck as elongate, flat projections with intervening deep pits. Deck area flattened with thin callus. Numerous minute and closely spaced growth lines on body whorl.

Holotype: UCMP 398607.

Type locality: UCMP loc. B-2368, Dip Creek, at the narrows, south shore of Lake Nacimiento, San Luis Obispo County, central California, 120°55'40"N, 35°43'45"W.

Discussion: The specimen has been damaged. The abrupt change in coiling of the body whorl is attributable to post-burial compression. The deck has been broken off from its juncture with the anterior part of the aperture and pushed into the aperture. The entire deck has been displaced approximately 2 mm posteriorly. The deep pits surrounding the extensions of the four strongest teeth onto the deck are probably the result of absorption of shell material by the animal or post-mortum dissolution of the deck area. Neritids are known to resorb internal shell structures (WOODWARD, 1892; COSSMANN, 1925) and produce shells that are subject to differential dissolution. The neritid shell has an external layer of calcite and one or more inner layers of aragonite (BØGGILD, 1930; WILBUR, 1964). The inner lip callus is especially prone to post-mortum dissolution, and the genus *Otostoma* was originally characterized as lacking a neritid inner lip and columella (D'ARCHIAC, 1859) because the available specimens had undergone selective dissolution (BINKHORST, 1861).

The new species is most similar to *Otostoma divaricata* (D'ORBIGNY, 1847:pl. 4, figs. 43, 44), an apparently widely distributed species that has been reported from both the Upper Cretaceous of southern India (STOLICZKA, 1868: 340–341, pl. 23, figs. 11, 12; pl. 28, fig. 5) and Hungary (PETHÖ, 1906:127–130, pl. 9, figs. 11–17). KEEN & COX (1960:fig. 183, figs. 14, 14a) figured *O. divaricata* from the Upper Cretaceous of Hungary as the illustration for the genus *Otostoma*. STOLICZKA (1868) reported the latter species from the southern India "Arrialoore" Group, which is of Campanian to Maastrichtian age according to SASTRY *et al.* (1968). The age of *O. divaricata* in Hungary is Maastrichtian according to COSSMANN (1925:203). PETHÖ's illustrations of *O. divaricata* show that there is considerable variation in this species. Some of his specimens are similar to *O. aethes* in size and in having the following morphologic features: spiral ribs in the anterior third of the body whorl, collabral ribs much stronger than the spiral ribs, strong teeth on the inner lip, and an angulate shoulder on the body whorl. *Otostoma aethes* differs in having a larger dorsal surface, narrower and more elongate aperture, an



Explanation of Figures 2 to 4

Figures 2-4. *Otostoma aethes* Squires & Saul, sp. nov., holotype, UCMP 398607 from UCMP loc. B-2368, $\times 1.6$. Figure 2. Apertural view. Figure 3. Abapertural view, low-level lighting used to show subdued sculpture. Figure 4. Dorsal view.

inner lip callus apparently nearly flat, subequal teeth on the inner lip, and in being less globose with a shorter spire and a more angulate shoulder.

The flattened inner lip area renders *Otostoma aethes* an atypical *Otostoma*, but its collabral sculpture and the pattern of the teeth on the inner lip are not found in *Nerita*.

WENZ (1938) and DAVIES (1971) reported the geologic range of *Otostoma* to be Cretaceous to Paleocene and its distribution to be cosmopolitan. GLIBERT (1962), however, reported *O. equinus* (Bezançon, 1870) from the middle Eocene (Lutetian) of the Paris Basin, France. Most workers have assigned *equinus* to *Velates* Montfort, 1810, which is closely allied with *Otostoma*. WOODS & SAUL (1986) also believed that *equinus* and probably *Velates noorpoorensis* (d'Archiac & Haime, 1854) of the Eocene of India should be placed in *Otostoma*. *Velates batequensis* Squires & Demettrion, 1990, from the lower Eocene of Baja California Sur, Mexico, is also very closely allied to *Equinus*. Juvenile specimens of *equinus* have characteristics of *Otostoma* whereas adult specimens have characteristics of *Velates*. More work is needed to fully resolve the taxonomic position of these ribbed neritids.

Otostoma is a Tethyan genus and most species are from the Old World Tethyan paleobiogeographic province. Previously, the only report of *Otostoma* from the Pacific coast of North America was that of ALLISON (1955:414, pl. 40, figs. 11, 12), who reported specimens of the Japanese species *Otostoma japonicum* (Nagao, 1934) from the Middle Cretaceous (upper Aptian, Alisitos Formation) of Baja California, Mexico. Allison's figured specimen has a concave ramp area and a noded shoulder; it is smaller, has a more elevated spire, and has stronger collabral ribs on the spire than *O. aethes*. As mentioned by WOODS & SAUL (1986), neither Allison's figured specimen nor "*Otostoma*" *japonicum* (Nagao) belong to *Otostoma*; both belong instead to the genus *Corsania* Vidal, 1917. The Alisitos Formation

material differs enough from *Corsania japonicum* to constitute a new species. *Desmieria peruviana* Olsson, 1934, from the Late Cretaceous of the Amotape region, Peru, is also a *Corsania*. The genus *Otostoma* is closely related to *Corsania*, but in *Corsania* the spiral sculpture is dominant, especially about the mid-whorl, the whorl is distinctly angulate rather than globular in profile, and the angulations are emphasized by strong nodes. DOUVILLÉ (1904) recognized these two groups but retained both within *Desmieria* [= *Otostoma*]. A number of species of *Corsania*, including Allison's species from the Alisitos Formation and *Corsania japonica* (Nagao) from Japan, will need to be reallocated before the geologic range and paleogeographic distribution of *Otostoma* can be more accurately understood.

Additional species of *Otostoma* in the United States are *O. apparatus* Cragin, 1893 [as *Neritina*], *O. marcouana* Cragin, 1895 [as *Neritoma*], and *O. pecosensis* Stanton, 1947 [as *Nerita*?]. All are from Lower Cretaceous (Comanchian Series) of Texas and are discussed and illustrated in STANTON (1947). Unlike the new species, all are very small and have a fairly elevated spire and a more rounded shoulder on the body whorl.

Other nerites known from Cretaceous strata of the Pacific coast of North America are *Nerita (Bajanerita) californiensis* (White, 1885) and *Neritina (Dostia) cuneata* (Gabb, 1864). The subgenus *Bajanerita* Squires, 1993, present in the Rosario Formation of early Maastrichtian age in Baja California, Mexico, is characterized by its small size, only three very wide but strong teeth on the inner lip, and many small teeth on the outer lip. WOODS & SAUL (1986) suggested placing *Nerita cuneata* Gabb, 1864, in *Neritina (Dostia)* rather than *Velates*, where STEWART (1927) had placed it.

The only Paleocene nerite reported from the Pacific coast of North America is a possible new species of *Nerita*

(*Theliostyla*) said to be from the Sepultura Formation near Punta Rosario, Baja California, Mexico (WOODS & SAUL, 1986). It is much smaller than *Otostoma aethes*, has 18 granulate spiral ribs on the body whorl, and has numerous teeth on the outer lip. As mentioned by SQUIRES (1992), Eocene strata of the Pacific coast of North America, of the Paris Basin, France, and of Hungary have also yielded various species of *Nerita* (*Theliostyla*). They share similar features that differentiate them from *O. aethes*.

Otostoma aethes sp. nov. is the only neritid known from strata of latest Maastrichtian to earliest Paleocene age on the Pacific coast of North America. It is also the only *Otostoma* known from this region and may indicate a very late Maastrichtian Tethyan-influenced influx of warm-water conditions at the K/T boundary.

Etymology: The name is derived from the *aethes*, Greek, meaning unusual or strange.

Occurrence: Latest Maastrichtian or possibly earliest Paleocene, unnamed strata, Dip Creek, south shore of Lake Nacimiento, San Luis Obispo County, central California.

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The Nautilid *Eucymatoceras* (Mollusca: Cephalopoda) in the Lower Cretaceous of Northern California

by

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Abstract. Three specimens of the nautilid *Eucymatoceras plicatum* (Fitton, 1836), characterized by chevron-shaped ribs, were collected from Lower Cretaceous (Aptian) rocks in northern California. This is the first record of the genus in California, and the second record in the Western Hemisphere. Previous records are from the Lower Cretaceous (Barremian and Aptian) of western and southeastern Europe and Baja California, Mexico.

INTRODUCTION

Among the numerous Cretaceous fossils collected during our many years of field work in the Cottonwood District of northern California are three specimens of the distinctive nautilid cephalopod *Eucymatoceras*. Two specimens are in the geology collections of the California Academy of Sciences (CASG); the third is from the former collections of the University of California, Los Angeles (UCLA), now at the Department of Invertebrate Paleontology, Los Angeles County Museum of Natural History (LACMIP). The purpose of this paper is to describe these specimens and compare them with previously described specimens.

SYSTEMATIC PALEONTOLOGY

MOLLUSCA

CEPHALOPODA

Family CYMATOCERATIDAE Spath, 1927

Genus *Eucymatoceras* Spath, 1927

Type species: *Nautilus plicatus* Fitton, 1836; by original designation (SPATH, 1927).

Diagnosis: Conch rounded, depressed; suture slightly sinuous, siphuncle subcentral; prominent coarse ribs in a chevron pattern with the principal V's pointing adapically on the venter and adorally on the flanks.

Discussion: Three species of *Eucymatoceras* were recognized by KUMMEL (1956:433) and by SHIMANSKY (1960:243–244): *E. plicatum* (Fitton, 1836) [= *E. requienianus* (d'Orbigny, 1840)], *E. stschurowskii* (Milashevich, 1877), and *E. steveni* (Karakasch, 1907). KUMMEL (1956:433) notes that these three species have similar shaped shells,

but he doubts that conch form in *Eucymatoceras* can be considered as species diagnostic. He mentions no other distinguishing characteristics. From published descriptions and illustrations, *E. stschurowskii* and *E. steveni* appear to differ from *E. plicatus* in the character of the ribbing. In *E. stschurowskii* the ribs are not straight and uniform but are irregularly angled in zig-zag fashion across the flank (MILASHEVICH, 1877:pl. 1, fig. 11). *Eucymatoceras steveni* differs in having an additional short chevron on the venter with the V pointing adorally, forming five chevron angles in all compared to the two chevron angles on other specimens of this genus. These distinctions are summarized by SHIMANSKY (1960:243–244).

Our specimens and published illustrations of *Eucymatoceras* demonstrate considerable variation in ribbing pattern including small chevrons intercalated between the larger ones, reversed rib angulation at the apertural flank edge, irregular truncation of ribs (incomplete chevrons), chevron number, chevron angle, and position of the chevron on the flank. Chevron angles measured from published illustrations and from the California specimens vary from 45 to 80° on the venter and 30 to 95° on the flanks (Table 1). The position of the flank chevron varies from mid-flank to ventrolateral.

The variability in rib character expression, and placement do not appear to define consistent species-level groups. The three taxa (*Eucymatoceras fittoni*, *E. stschurowskii*, and *E. steveni*) are based on differences in ribbing that we interpret as variation in a single species. Published descriptions and available specimens do not uniquely resolve this taxonomic problem.

Occurrence: The genus is reported from Barremian and Aptian strata in England (FITTON, 1836; KUMMEL, 1956), France (D'ORBIGNY, 1840; KILIAN & REBOUL, 1915), Spain

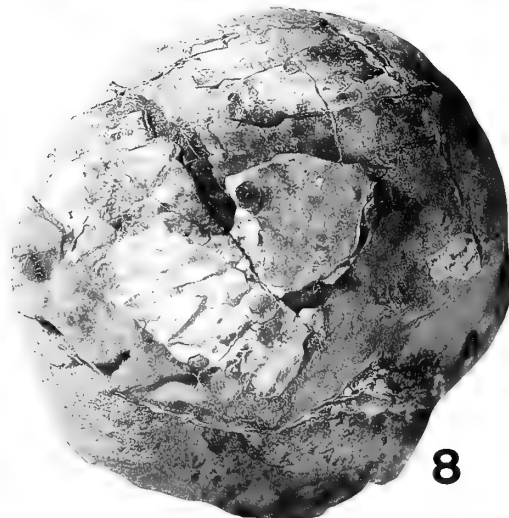
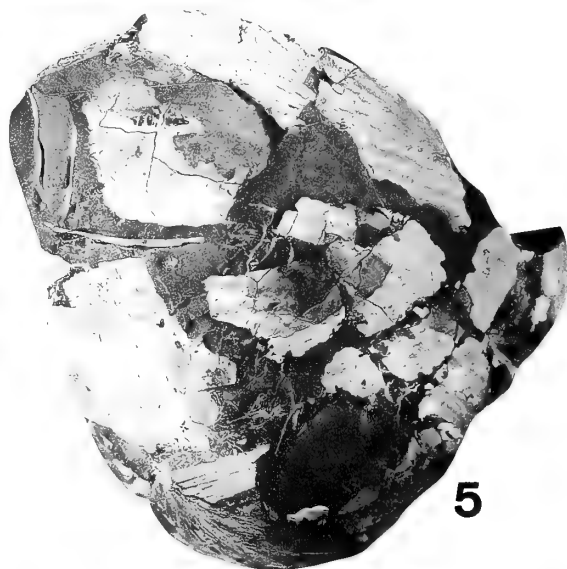
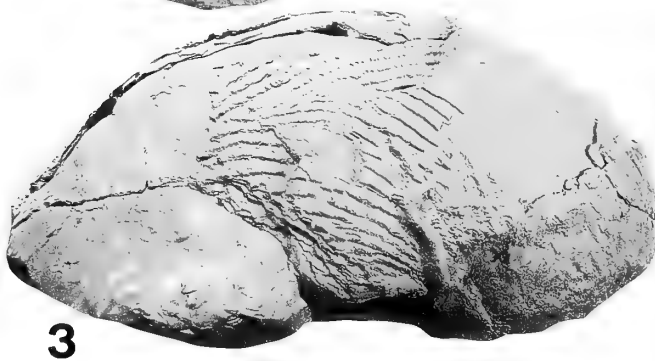
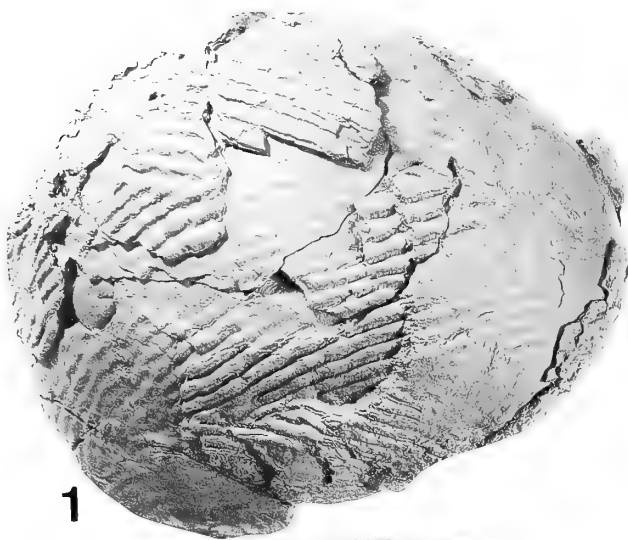


Table 1

Chevron angles (degrees) of specimens of *Eucymatoceras*. Measurements were made directly from CASG and LACMIP specimens; the remainder are from published illustrations.

	Flank chevron (degrees)	Ventral chevron (degrees)
CASG 60847.01	30	45
CASG 60847.02	56	29, 38
LACMIP 12100	—	30
FITTON, 1836	55–60	55–60
D'ORBIGNY, 1840	88–95	59–60
MILASHEVICH, 1877	95–100	—
UHLIG, 1883	40–58	—
KARAKASCH, 1907	70–90	80–90
KUMMEL, 1956	65–76	75–80
SHIMANSKY, 1960:pl. 5	64–71	—
DIMITROVA, 1967	40	60
CALZADA & VIADER, 1980	59	47
SUNDBERG, 1984	—	28, 30

(BATALLER, 1962; CALZADA & VIADER, 1980), Czechoslovakia (UHLIG, 1883), Bulgaria (DIMITROVA, 1967), Crimea (MILASHEVICH, 1877; KARAKASCH, 1907), Caucasus (SHIMANSKY, 1960), Mexico (SUNDBERG, 1984), and California (herein).

Eucymatoceras Plicatum (Fitton, 1836)

(Figures 1–8)

Nautilus plicatus FITTON, 1836: 129, fig. 1; Uhlig, 1883:178, pl. 3.

Nautilus requienianus D'ORBIGNY, 1840:72–74, pl. 10.

Nautilus stschurowskii MILASHEVICH, 1877:121–122, pl. 1, fig. 11.

Nautilus steveni KARAKASCH, 1907:30, pl. 2, fig. 13, pl. 8, fig. 12.

Eucymatoceras plicatus (Fitton): KUMMEL, 1956:432, text-fig. 27, pl. 21; DIMITROVA, 1967:17, pl. 1, figs. 1, 1a; CALZADA & VIADER, 1980: 164, pl. 2, figs. 2a, b.

Eucymatoceras plicatum Fitton: SHIMANSKY, 1960:243, pl. 5, figs. 2, 3a–b.

Eucymatoceras steveni Karakasch: SHIMANSKY, 1960:243, pl. 6, figs. 1a–b.

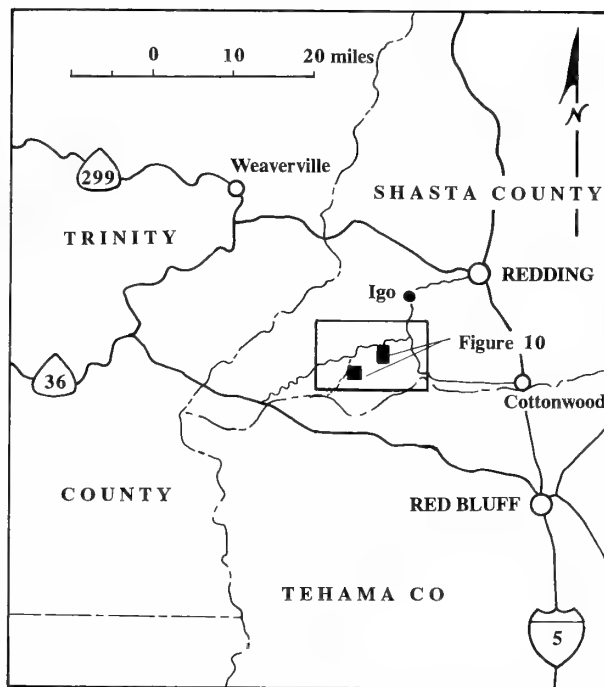


Figure 9

Map showing area of the Ono quadrangle (1:25,000) (open rectangle) and locations of the large scale maps of Figure 10.

Eucymatoceras stschurowskii Milashevich: SHIMANSKY, 1960: 244, pl. 8, figs. 2a–b.

Eucymatoceras sp.: SUNDBERG, 1984:43–46, fig. 2.

Description and diagnosis: As for genus.

Description of northern California specimens: Specimens are crushed, distorted, and partly eroded fragments from 150 mm to 230 mm in maximum dimension.

The best preserved specimen, CASG 60847.01 (Figures 1–4), is part of outer whorl, mostly body chamber, maximum dimension 230 mm; inner whorls crushed, exposed in erosional cross section; four partial suture lines are straight to slightly sinuous; siphuncle not visible; ribs about 3.5 mm wide, generally broadly arcuate, flat-topped and steep-sided in cross section; interspaces about 2 mm wide; chevron angles on venter and on flank about 45° and 30°.

Explanation of Figures 1 to 8

Figures 1–4. *Eucymatoceras plicatum* (Fitton, 1836). CASG 60847.01, maximum dimension 230 mm. Figure 1. Ventral view. Figure 2. Ventral view from adapical end. Figure 3. Lateral view. Figure 4. Ventral view from adoral end.

Figure 5. *Eucymatoceras plicatum* (Fitton, 1836). CASG 60847.02, maximum diameter 207 mm. Lateral view.

Figures 6, 7. *Eucymatoceras plicatum* (Fitton, 1836). Private collection, present status unknown, maximum diameter (estimated) 250 mm.

Figure 8. *Eucymatoceras plicatum* (Fitton, 1836). LACMIP 12100 (from UCLA 2972 = LACMIP 22972), maximum dimension 150 mm. Ventrolateral view.

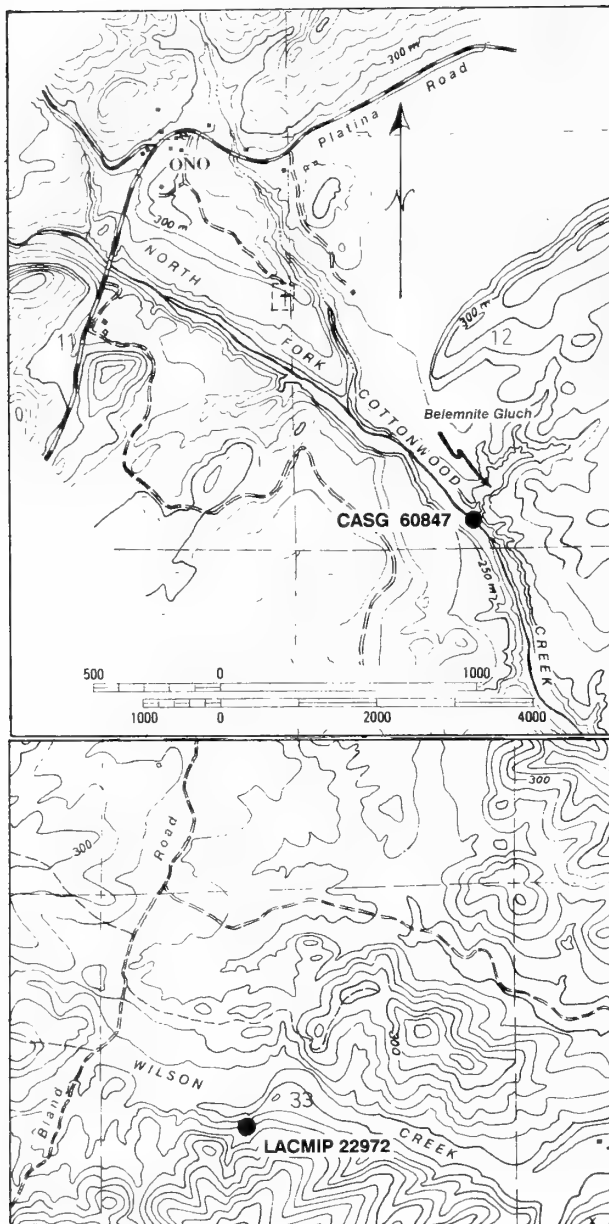


Figure 10

Maps of collecting localities, California Academy of Sciences Geology 60847 and Los Angeles County Museum Invertebrate Paleontology 22972. Base map is the Ono 1:25,000-scale metric topographic map (1981), contour interval 10 m.

respectively (measurement of chevron angles is illustrated in Figure 11). Most ribs extend singly from umbilical edge, some bifurcate on inner flank; umbilical and peripheral ribs irregularly truncate one another (incomplete chevrons), a feature well-shown in published illustrations (UHLIG, 1883:pl. 3; KUMMEL, 1956:pl. 21) (see Figure 11).

A second specimen, CASG 60847.02 (Figure 5), is a

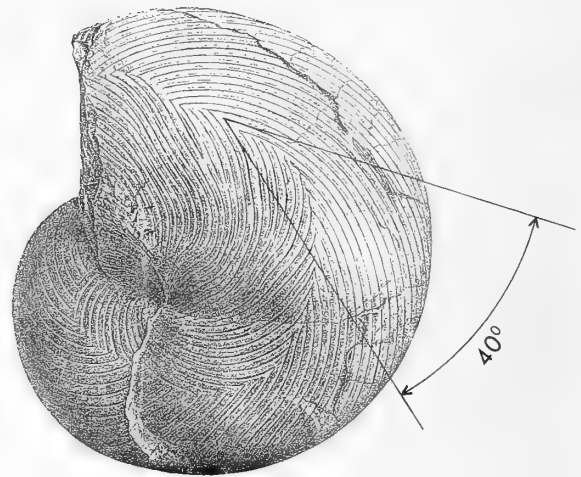


Figure 11

Illustration of measurement of chevron angles of ribs on *Eucymatoceras*; measurement taken at apex of angle. Chevron angle changes irregularly with growth and increases as ribs curve from apex. Figure of *E. plicatus* from UHLIG (1883).

nearly complete whorl, maximum diameter 207 mm, severely crushed laterally with chevron ribs showing on three shell fragments near the apertural end of the conch. Chevron angles on ventral shell fragments are 29 and 38°; angle on flank shell fragment is 56°. Suture not exposed.

The smallest specimen, LACMIP 12100 (from UCLA locality 2972 = LACMIP 22972) (Figure 8), maximum dimension 150 mm, is crushed and eroded with partial cross section of inner whorls exposed on inner side. Chevron angle on one ventral shell fragment is 30°.

A fourth, exceptionally well-preserved specimen (Figures 6, 7), from the North Fork of Cottonwood Creek, Shasta County, was collected by a local resident and was photographed in 1951 by M. A. Murphy. The present location of this specimen is unknown.

Remarks: The California specimens generally have smaller chevron angles than those measured from published illustrations (Table 1).

Localities: The northern California specimens came from the Budden Canyon Formation, upper Chickabally Member (MURPHY *et al.*, 1964), Cottonwood District, southwest Shasta County, California (Figures 9, 10).

CASG Locality 60847: Creek-bed exposure on the north side of the North Fork of Cottonwood Creek, 5 m upstream from the mouth of Belemnite Gulch, a small north-heading tributary (Figure 10). Two specimens (Figures 1–5). C. Schuchman and M. A. Murphy, collectors.

LACMIP Locality No. 22972 [= UCLA 2972]: Exposure in south-heading tributary to Roaring River, approximately ½ mile (1 km) east of Bland Road (Figure 10; MURPHY, 1956:fig. 4). One specimen. M. A. Murphy, collector.

Age: All specimens are associated with or bracketed by fossils from the *Gabbiceras wintunius* zone, Upper Aptian (Gargasian) (MURPHY, 1956; MURPHY *et al.*, 1964).

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We thank several individuals and agencies for their help. Stephen Schuchman and George Shkurkin provided English translations of Russian and Bulgarian publications. J. Latini and L. Westlake permitted physical access to the area. The National Science Foundation, U.S. Army Corps of Engineers, California Department of Water Resources, and University of California Riverside Intramural Research Fund provided financial support for the larger project of which this paper is a part.

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Earliest Record of the Anomiid Bivalve *Pododesmus*: A New Species from the Lower Eocene of Western Washington

by

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Abstract. An anomiid bivalve, *Pododesmus* (*Pododesmus*) *dunhamorum* sp. nov., from lower Eocene shallow-marine strata in the upper part of the Crescent Formation on the west side of Dabob Bay, Jefferson County, eastern Olympic Peninsula, Washington, is the earliest known species of this genus and subgenus. The new species is one of two Eocene species of *Pododesmus* s.s. that inhabited hard substrate in nearshore waters along the Pacific coast of North America. The other species is *P. (P.) inornatus* (Gabb, 1864) from the middle Eocene of central California and southwestern Washington.

INTRODUCTION

Pododesmus sensu stricto (Bivalvia: Anomiidae) is known only from a few Tertiary fossil species in the Americas and New Zealand and two extant species in the Americas. The most widespread living species is *Pododesmus* (*P.*) *rudis* (Broderip, 1834), which is found byssally attached to rock, coral, shell, or other hard substrates in shallow waters along the coasts of South Carolina, Florida, Texas, Bermuda, West Indies, Brazil, and central Argentina (CARCELLES, 1941; ABBOTT, 1974; RIOS, 1975). According to ABBOTT (1974) and RIOS (1975), *Pododesmus leloiri* Carcelles, 1941, from the Golfo San Matias, Argentina, is probably a synonym of *P. (P.) rudis*. The only other undoubted living species of *Pododesmus* s.s. is *P. (P.) foliatus* (Broderip, 1834), which ranges from western Mexico to northern Peru (KEEN, 1971).

Described herein is a new species of *Pododesmus* s.s. from lower Eocene strata in the upper part of the Crescent Formation, western Washington (Figure 1). This is the earliest record of this genus and subgenus. Previously, the earliest record of *Pododesmus* s.s. was from middle Eocene strata in central California and western Washington (WEAVER, 1942 [1943]).

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACM and LACMIP, Natural History Museum of Los Angeles County, Los Angeles, Malacology Section and Invertebrate Paleontology Section, respectively; UCMP, University of California Museum of Paleontology.

STRATIGRAPHIC DISTRIBUTION AND GEOLOGIC AGE

Pododesmus (*P.*) *dunhamorum* sp. nov. was found at three localities in the upper part of the Crescent Formation along the west side of Dabob Bay about 50 km west of Seattle, Jefferson County, Washington (Figure 1). Localities CSUN 1511 and 1512 are very near each other, and CSUN loc. 1502 is approximately 6 km farther north. Thirty-nine specimens were found, four at loc. 1502, 22 at loc. 1511, and 13 at loc. 1512. All are single valves; four left valves, 12 right valves, and 23 of which the valve type cannot be determined. Preservation ranges from poor to good, and at loc. 1511, 40% of the specimens are molds.

The lithologies at CSUN locs. 1511 and 1512 and their depositional environment and geologic age are discussed by SQUIRES *et al.* (1992). At both localities, there is fossiliferous pebble conglomerate interbedded with basalt units that were extruded into very shallow-marine waters. Erosion of the basalts by storm waves produced rubble that was transported offshore, where substrate-attaching species, like *Pododesmus* (*P.*) *dunhamorum*, were able to inhabit it. The upper Crescent Formation in this area is late early Eocene in age on the basis of its contained calcareous nannofossils, benthic foraminifera, and macrofossils. This age is equivalent to calcareous nannofossil Zones CP10-CP11, which straddle the boundary between the provincial molluscan "Capay Stage" and "Domengine Stage."

Fossils from CSUN loc. 1502 were collected from boul-

der-sized blocks of Crescent Formation that are within a modern landslide. The strata at this locality are lithologically, macrofaunally, and paleoenvironmentally similar to those at CSUN locs. 1511 and 1512. The rocks in the two areas are coeval (SQUIRES, 1992).

SYSTEMATIC PALEONTOLOGY

Family ANOMIIDAE Rafinesque, 1815

Genus *Pododesmus* Philippi, 1837

Type species: *Pododesmus decipiens* Philippi, 1837 [= *Placunanomia rudis* Broderip, 1834], by monotypy; Recent, South Carolina to Argentina.

Subgenus *Pododesmus* s.s.

Pododesmus (Pododesmus) dunhamorum
Squires, sp. nov.

(Figures 2–9)

Anomiid (*Pododesmus*-like, new genus?): SQUIRES *et al.*, 1992: 7, table 1, pl. 1, figs. 28–29.

Diagnosis: Medium-sized *Pododesmus*, ovate, sculpture of 15 to 17 radial ribs on both valves; byssal foramen small, closed by a calcareous plug immediately adjacent to moderately elevated crurum.

Description: Medium-sized *Pododesmus*, reaching 24 mm in height, ovate, slightly inequivalved with left (free) valve more inflated, slightly inequilateral, beaks central, shell thin. Left valve with approximately 15 to 17 low, somewhat irregular radial ribs; interior margin of valve flattened. Right valve with attachment scar covering anterior one-fourth of valve, remainder of valve with approximately 15 to 17 radial ribs, spinose near ventral margin of valve. Radial ribs smaller and more crowded anteriorly. Right valve with small byssal foramen, encircled by a low rim; lower half of byssal foramen plugged by a calcareous deposit. Foramen situated beneath and immediately adjacent to a moderately elevated crurum (= chondrophore). Crurum with a narrow slot for resilium. Interior of right-valve margin somewhat flattened.

Holotype: LACMIP 11515.

Type locality: CSUN loc. 1511, 47°44'45"N, 122°51'06"W.

Paratypes: LACMIP 12227–12229; all from CSUN loc. 1511.

Dimensions: Of holotype, height 20.9 mm, length 18.1 mm; paratype 12227, height 16 mm, length 14.5 mm; paratype 12228, height 24 mm, length 20 mm; paratype 12229, height 17 mm, length 16 mm.

Discussion: The new species is assigned to *Pododesmus* s.s. on the basis of the combination of the following features: radial sculpture on both valves, small plugged byssal foramen, and the unnotched dorsal margin of the relatively

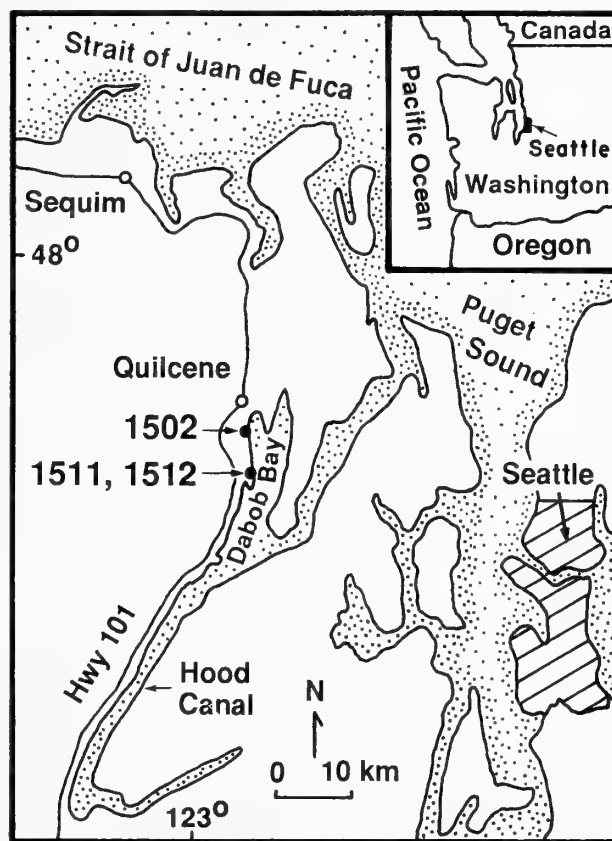
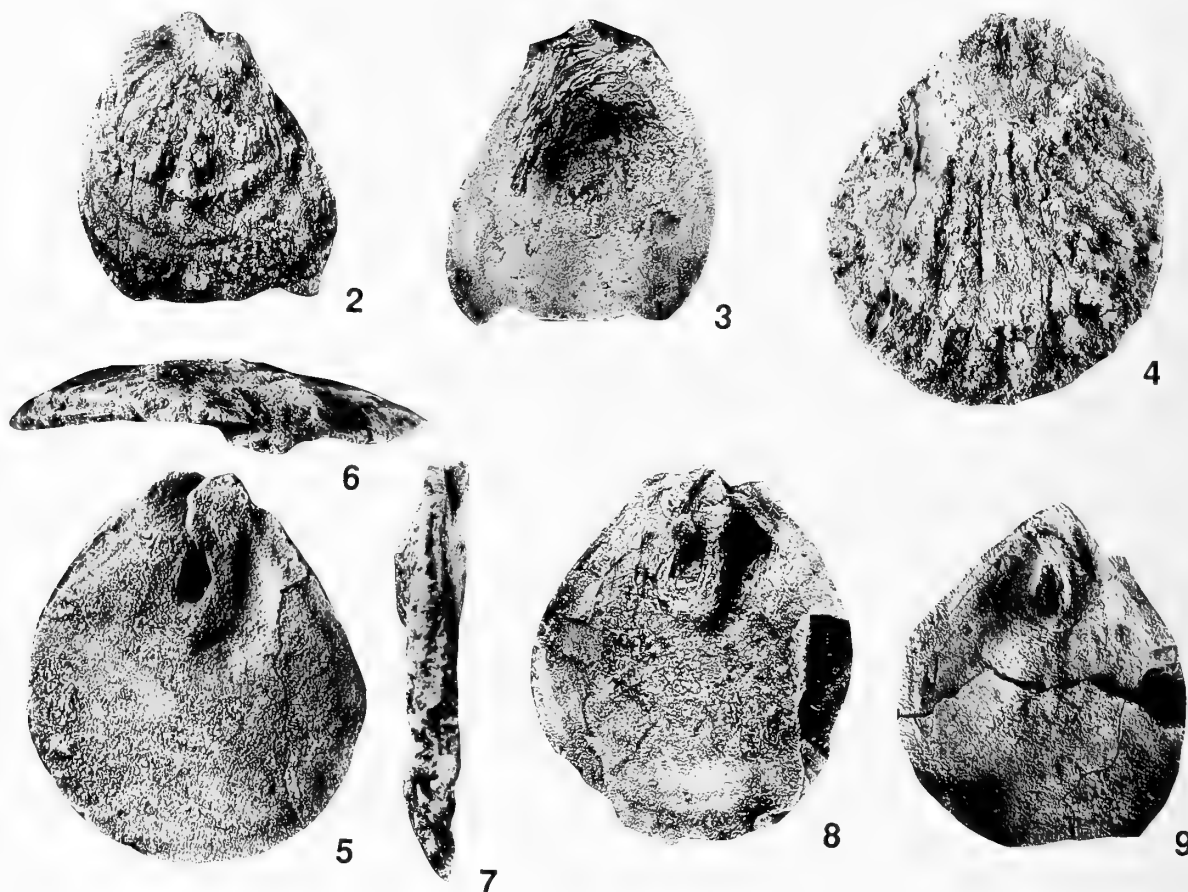


Figure 1

Location map for localities of *Pododesmus (Pododesmus) dunhamorum* Squires, sp. nov.

thick right valve. The new species is remarkably similar to *Pododesmus (P.) decipiens*, the type species of *Pododesmus* s.s., and especially to specimens (LACM 78-95, LACM 78-96) of the type species from Golfo San Jose, Chubut Province, Argentina. OLSSON & PETIT (1964:529–530, pl. 77, fig. 1) gave a detailed description of *Pododesmus (P.) rudis* (Broderip, 1834), the junior subjective synonym of *P. (P.) decipiens*, and figured the interior of the right valve. CARCELLES (1941:pl. 1, figs. 1, 2) and KEEN (1969:fig. C103 12a, b) also provided illustrations of *P. (P.) rudis*.

The shell of *Pododesmus* is morphologically similar to that of *Anomia* Linné, 1758, the main distinction being that *Pododesmus* has two muscle scars in the central “white area” on the interior of the left valve rather than three, as in *Anomia* (BEU, 1967; KEEN, 1969). Also, in *Pododesmus* both valves are radially sculptured, opaque, and fairly thick, whereas in *Anomia* the right valve lacks radial sculpture and both valves are translucent and usually thin (BEU, 1967). *Pododesmus* is further distinguished by a byssal foramen that may be partially or entirely closed and which does not open as a slit at the dorsal margin, and a byssal plug that may be retained within the foramen (BEU, 1967; KEEN, 1969). Although the muscle scars on the left valve are not preserved in the new species, the overall mor-



Explanation of Figures 2 to 9

Figures 2-9. *Pododesmus (Pododesmus) dunhamorum* Squires, sp. nov., CSUN loc. 1511. Figures 2-3: paratype, LACMIP 12227, left valve, $\times 2.6$; Figure 2, exterior; Figure 3, interior. Figures 4-7: holotype, LACMIP 11515, right valve, $\times 2.5$; Figure 4, exterior; Figure 5, interior; Figure 6, dorsal view of hinge line; Figure 7, anterior view. Figure 8: paratype, LACMIP 12228, right-valve interior, $\times 2.2$. Figure 9: paratype, LACMIP 12229, right-valve interior, $\times 2.4$.

phology of both valves is in keeping with features of *Pododesmus* rather than of *Anomia*.

Pododesmus is anatomically the most primitive living anomiid (YONGE, 1977, 1980), and it probably evolved into *Anomia* (YONGE, 1977). Using shell microstructure of primarily the right valve, CARTER (1990) subdivided the anomiids into three groups. The only species of *Pododesmus* that he studied was the living *Pododesmus (Monia) macrochisma* (Deshayes, 1839), and he included it among the "*Anomia simplex* group" that is characterized by a right valve with an outer layer of calcitic simple prisms and inner layers of aragonite and a left valve that always has a prominent layer of foliated structure. This group represents a primitive microstructure grade that is compatible with the primitive soft anatomy of *P. (M.) macrochisma* (CARTER, 1990).

KEEN (1969) recognized four subgenera in *Pododesmus*: *Pododesmus* s.s., *Monia* Gray, 1850, *Heteranomia* Winck-

worth, 1922, and *Tedinia* Gray, 1853. The only two subgenera with a known fossil record are *Pododesmus* s.s. and *Monia*. KEEN (1969) distinguished these two genera on the basis of the size of the byssal foramen, with *Pododesmus* having a much smaller one. HERTLEIN & GRANT (1972) reported *Pododesmus* as having thicker valves and a smaller foramen than *Monia*, and that the foramen is always plugged in *Pododesmus* but is usually open in *Monia*. BEU (1967) considered *Monia* to be a distinct genus and not a subgenus of *Pododesmus*. He noted that the right valve of *Pododesmus* is considerably thicker than the very thin right valve of *Monia* and that the byssal plug is small and permanently fused into the shell in *Pododesmus*, whereas in *Monia* the byssal plug is large, thin, and completely free. Further, in *Pododesmus* the crurum is approximately triangular, with anterior and posterior dorsal resilial surfaces, whereas in *Monia* the crurum has only a single dorsal resilial surface. Although the crurum of the new species is not well pre-

served and is incomplete even on the holotype, the other morphologic features indicate placement in *Pododesmus* s.s. rather than in *Monia*.

The new species is similar to *Pododesmus paucicostatus* BEU (1967:240, pl. 1, fig. 3; pl. 2, figs. 6, 9, 10; text-figs. 2a, d) from the middle Miocene of New Zealand (BEU & MAXWELL, 1990). Beu's species has all the diagnostic features of *Pododesmus* s.s. and is judged herein to be assignable to *Pododesmus* s.s. The new species differs from Beu's species in the following features: smaller valve size, thinner valves, and smaller byssal foramen.

The new species is also similar to *Paranomina scabra* (MORTON, 1834; WADE, 1926:67–68, pl. 22, figs. 3–9) from Upper Cretaceous strata in the southeastern part of the United States. The new species, however, is smaller, it has coarser and more closely spaced radial ribs, and a byssal foramen is located much closer to the crurum and lacks the long linear scar between the foramen and the crurum.

Only two other Eocene anomiid species are known from the Pacific coast of North America. One is *Pododesmus inornatus* (GABB, 1864:217, pl. 32, figs. 288, 288a) from the middle Eocene in central California and southwestern Washington (STEWART, 1930; VOKES, 1939; WEAVER, 1942 [1943]; KEEN & BENTSON, 1944; MOORE, 1987). VOKES (1939:57–58, pl. 3, figs. 6, 7, 9, 11) assigned *P. inornatus* to *Pododesmus* (*Monia*). Only one of the figured specimens (UCMP hypotype 15587, see VOKES, 1939:pl. 3, fig. 6) shows the interior of the right valve of *P. inornatus*. The byssal foramen and crural area are very similar to that of the new species, and I believe that *P. inornatus* should be placed in *Pododesmus* s.s. and not in *Monia*. The only other figured specimen of *P. inornatus* that shows the byssal foramen area is UCMP hypotype 15589 (see VOKES, 1939:pl. 3, fig. 11), but only the exterior of the right valve is free of matrix. Vokes' illustration is misleading because it gives the impression that the foramen is free of matrix. The area around the foramen has been excavated, and the border of the foramen is no longer present. It is impossible to tell what the exact diameter of the foramen was, and the larger diameter may be an artifact. Nevertheless, the foramen is smaller than that normally present on specimens of *Monia*. *Pododesmus* (*P.*) *dunhamorum* differs from *Pododesmus* (*P.*) *inornatus* (Gabb, 1864) in having a less-inflated left valve, fewer but much stronger radial ribs on the left valve, an ornamented right valve, and in lacking commarginal riblets or lamellae on the left valve.

The other reported Eocene anomiid from the Pacific coast of North America is *Anomia mcgoniglenensis* HANNA (1927:278, pl. 31, figs. 1, 2, 5, 7), from middle Eocene ("Domengine Stage") strata of the San Diego area, southern California, to southwestern Oregon (KEEN & BENTSON, 1944; TURNER, 1938; WEAVER, 1942 [1943]; GIVENS & KENNEDY, 1976; SQUIRES, 1984, 1989; MOORE, 1987). VOKES (1939) questionably put *A. mcgoniglenensis* into synonymy with *Pododesmus* (*Monia*) *inornatus* because the range in coarseness of sculpturing in *A. mcgoniglenensis* over-

laps with that observed in *P. (M.) inornatus*. GIVENS & KENNEDY (1976), however, established *A. mcgoniglenensis* as a species of *Anomia*, on the basis of well-preserved left valves that show three, rather than two, muscle scars.

The only other Pacific coast of North America Paleogene anomiid species that has been assigned to *Pododesmus sensu lato* is *P. newcombei* CLARK & ARNOLD (1923:141, pl. 21, figs. 3–6; WEAVER, 1942 [1943]: 100–101, pl. 23, figs. 2, 3, 5) from the upper Oligocene Sooke Formation, on southern Vancouver Island, British Columbia. The interior of this species is unknown, but *P. (P.) dunhamorum* differs from it by having a much flatter right valve, coarser radial ribs, and fewer and more widely spaced radial ribs. CLARK & ARNOLD (1923) noted that *P. newcombei* is similar to *P. macrochisma* (Deshayes, 1839) [= *P. cepio* (Gray, 1850)]. Modern workers assign Deshayes' species to the subgenus *Monia*. *Pododesmus* (*Monia*) *macrochisma* ranges today along the Pacific coast of North America and in Japan, and is known as a fossil from rocks as old as late Miocene (MOORE, 1987).

By late Eocene, *Pododesmus* s.l. was present in New Zealand, and *Pododesmus* s.s. lived there from Oligocene through middle Miocene (BEU, 1967; BEU & MAXWELL, 1990). IHERING (1907) reported four species of *Pododesmus* from the Patagonian Formation in Patagonia, southern Argentina, and DAVIES (1975) considered this formation to be early Miocene in age. HERTLEIN & GRANT (1972), however, concluded that Ihering's generic assignment of his four species is tenuous because of their poor preservation. *Pododesmus* (*P.*) *rudis* has been reported from Pliocene rocks in Venezuela (WEISBORD, 1964). *Pododesmus* s.l. was present along the Gulf Coast of North America by the early Pleistocene (OLSSON & PETIT, 1964; WARD & BLACKWELDER, 1987) and today persists there as *P. (P.) rudis*, which also lives in the West Indies and along much of the western Atlantic coast of South America. GARDNER's (1926) report of *P. (P.) rudis* from the upper lower Miocene Chipola Formation in Florida and a report of this species from the lower Pleistocene Waccamaw Formation in North Carolina could not be substantiated by WEISBORD (1964) and WARD & BLACKWELDER (1987), respectively.

The geologic range of *Pododesmus* s.s., previously reported as Miocene to Recent (KEEN, 1969; DAVIES, 1971), is emended herein as late early Eocene to Recent.

Etymology: The species is named for George and Cressie Dunham, whose cooperation made the discovery of this new species possible.

Distribution: Upper lower Eocene (near boundary between "Capay Stage" and "Domengine Stage"), upper Crescent Formation, west side of Dabob Bay, eastern Olympic Peninsula, Jefferson County, western Washington (CSUN locs. 1502, 1511, and 1512).

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George and Cressie Dunham (Pulali Point, Washington) kindly allowed access to private property in the Pulali

Point area (CSUN locs. 1511 and 1512) and made this and other studies possible. Most of the specimens of the new species were collected by James L. and Gail H. Goedert (Gig Harbor, Washington) and Keith L. Kaler (Olympia, Washington). Ross E. and Marion Berglund (Bainbridge Island, Washington) provided some of the specimens from CSUN loc. 1502.

David R. Lindberg (UCMP) loaned specimens of comparative material. Louella R. Saul (LACMIP) allowed access to the collections and loaned specimens of *Paranomia scabra*. Lindsey T. Groves and C. Clifton Coney (LACM) allowed access to modern specimens of anomniids. Lindsey T. Groves, George K. Kennedy (LACMIP), and Richard E. Petit (North Myrtle Beach, South Carolina) provided some key literature. James L. Goedert read an early version of the manuscript. George L. Kennedy and an anonymous reviewer critically read the manuscript.

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- CSUN loc. 1511. Pebble conglomerate, 63 m above base of stratigraphically lowermost sedimentary interbed found along seaciff on west side of Dabob Bay at Pulali Point, latitude 47°44'45"N, longitude 122°51'06"W, central part of section 18, T26N, R1W, U.S. Geological Survey, 7.5-minute, Seabeck, Washington quadrangle, 1953 (photorevised 1968), eastern Olympic Peninsula, Jefferson County, western Washington. Upper Crescent Formation. Age: Late early Eocene (near boundary between "Capay Stage" and "Domengine Stage"). Collectors: J. L. and G. H. Goedert and K. Kaler, 1989–1991. (See SQUIRES *et al.*, 1992:figs. 2, 3).
- CSUN loc. 1512. Same as the CSUN loc. 1511, except 106 m stratigraphically higher in section.

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Relict Shells of Subantarctic Mollusca from the Orange Shelf, Benguela Region, off Southwestern Africa

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Abstract. Subfossil shells of three locally extinct mollusk species of Subantarctic affinity have been found in sediments on the middle Continental Shelf (120–140 m depth) in the Benguela region off southwestern Africa. These are the venerid *Tawera philomela* (E. A. Smith), the ranellid *Sassia* (*Sassia*) *philomelae* (Watson), and the buccinid *Pareuthria fuscata* (Bruguère). All three presently live on the mid-Atlantic islands of Tristan da Cunha and Gough. The abraded, bored, and encrusted state of *T. philomela* shells, including algal borings, records their exposure as a shell gravel under high-energy conditions in the photic zone. Cores of sediments and a ^{14}C date of 13.5 kyr B.P. confirm that *T. philomela* abundantly populated coarse sands in the sample area during the low sea level (~ -100 m) of the late glacial. The shell condition of *P. fuscata* suggests it was a contemporary, while that of *S. philomela* indicates a higher position in the faunal succession of the sample area, most likely due to a greater depth preference. The dispersal of these species from the mid-Atlantic to Africa is consistent with glacial intensification of the circumpolar circulation and accords with previous work indicating enhanced opportunities for Southern Ocean dispersal during glaciations. This zonal dispersal compensates to some extent for Africa's lack of shelf connections to the subpolar benthic fauna. The specific means of dispersal remains speculative, as do the causes for the subsequent local extinction of the dispersed species.

INTRODUCTION

The occurrence of submerged subaerial and shallow-water sediments, with enclosed fossils from terrestrial, estuarine and shoreface environments, is a widespread feature of the continental shelves of the world (EMERY, 1968). The deepest of these relict sediments were deposited when sea level was lowered to about -130 m at the Last Glacial Maximum, while the subsequent recovery of sea level left in its wake a transgressive sheet comprising sands and gravels abandoned on the deepening shelf. Radiocarbon-dated, very shallow-water molluscan shells from relict sediments have been useful in estimating the deglacial rise of sea level, while occurrences of "warm" and "cold" species beyond their modern ranges are evidence for fluctuations in the temperature of coastal waters over this period (EMERY *et al.*, 1988; TAVIANI *et al.*, 1991). This paper documents the finding of shells of Subantarctic or Southern Ocean mollusks not previously recorded from the southwest African

continental shelf (Figure 1). Taphonomic and stratigraphic evidence is presented, showing that the most common species, a venerid, is associated with relict coarse-grained sediments related to glacially lowered sea level. The dispersal of the species over ~ 2900 km from the mid-Atlantic islands to the African coast is discussed.

SOURCE OF SAMPLES

On the Orange shelf off the west coast of southern Africa (Figure 1a), the shoreline deposits of the deglacial transgression are to a large extent covered by a coast-parallel Holocene mudbelt (Figure 1b) consisting primarily of terrigenous silts and clays transported southward from the Orange River by a poleward undercurrent beneath the Benguela Current (ROGERS, 1977; ROGERS & BREMNER, 1991). The mudbelt thins seaward, where it laps onto the middle shelf in the vicinity of the Last Glacial shoreline.

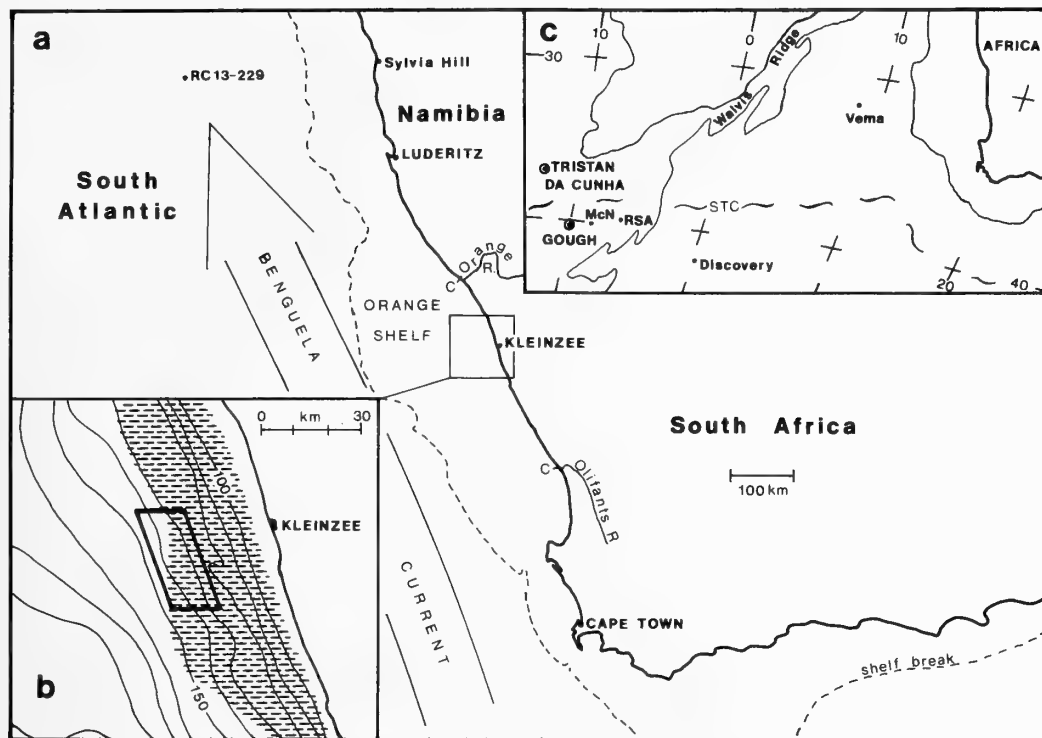


Figure 1

Figure 1a. West coast of southern Africa. Localities where *Concholepas concholepas* was obtained in Holocene beach sediments indicated by C. Figure 1b. Sample area off Kleinsee with bathymetry indicated at 10 m intervals and Holocene mudbelt shaded. Figure 1c. Southeast Atlantic Ocean showing mid-Atlantic islands, seamounts, and 3 km isobath. McN = McNish Seamount; STC = Subtropical Convergence.

There the coarse sands and gravels of the glacial shoreline are exposed or shallowly buried beneath the Holocene mud. The occurrence of these relict sediments was discussed by ROGERS (1977), who noted the presence of grain surface features typical of littoral sands. More recently, exploration of this terrain for diamonds has produced a suite of samples of dredged shells, made available courtesy of De Beers Marine (Pty) Limited and deposited in the South African Museum (SAM). Fifty-three samples were taken in an area off Kleinsee (Figure 1b). Bulk samples of shell were collected onboard the prospecting vessel, from the screens that exclude coarse gravel from the heavy-mineral concentration process. Additional specimens, mainly less common species, were also individually selected from the gravel screens. Taxa present in the bulk samples were identified, sorted, and counted. Documentation of the entire assemblage recovered, including methods of analysis, will be presented elsewhere (in preparation). Observations on shell condition were also made. A reconnaissance of the endolithic taxa infesting shells was accomplished by impregnating shells with polyvinylbutyrol (PVB) in acetone under low vacuum, then dissolving the shells in dilute HCl to reveal the cast borings. Relevant initial results are discussed here.

THE SUBANTARCTIC MOLLUSCA

Tawera philomela (E. A. Smith, 1885)

This venerid (Figure 2a-c) is the most abundant bivalve recovered from the sample area (34.4% of total bivalves). *Tawera philomela* occurs at the Southern Ocean islands of Tristan da Cunha, Gough, and South Georgia. A species of *Tawera* occurs on the west and east coasts of South America south of approximately 35°S, and at the Falkland Islands. Two species occur in southern Australia, two in New Zealand, and five species are distributed around the Subantarctic islands near New Zealand (DELL, 1964). New Zealand, with nine fossil species ranging from the Miocene, is evidently the distributional center of the genus (DELL, 1964). The record of *T. philomela* from South Georgia is mentioned only by DELL (1964), but because the molluscan fauna of this locality is Antarctic in character (POWELL, 1965), it should be viewed with some suspicion.

Tawera philomela has been recorded from a large range of depths: off Tristan at 7–12 m, 8–45 m, 117–104 m, and 1800 m (DELL, 1964; SOOT-RYEN, 1960; SMITH, 1885); off Nightingale Island at 180–280 m (SMITH, 1885); and off Gough at 90–140 m, 180 m, and 22 m (DELL, 1964; MELVILL & STANDEN, 1907, South African Museum Col-

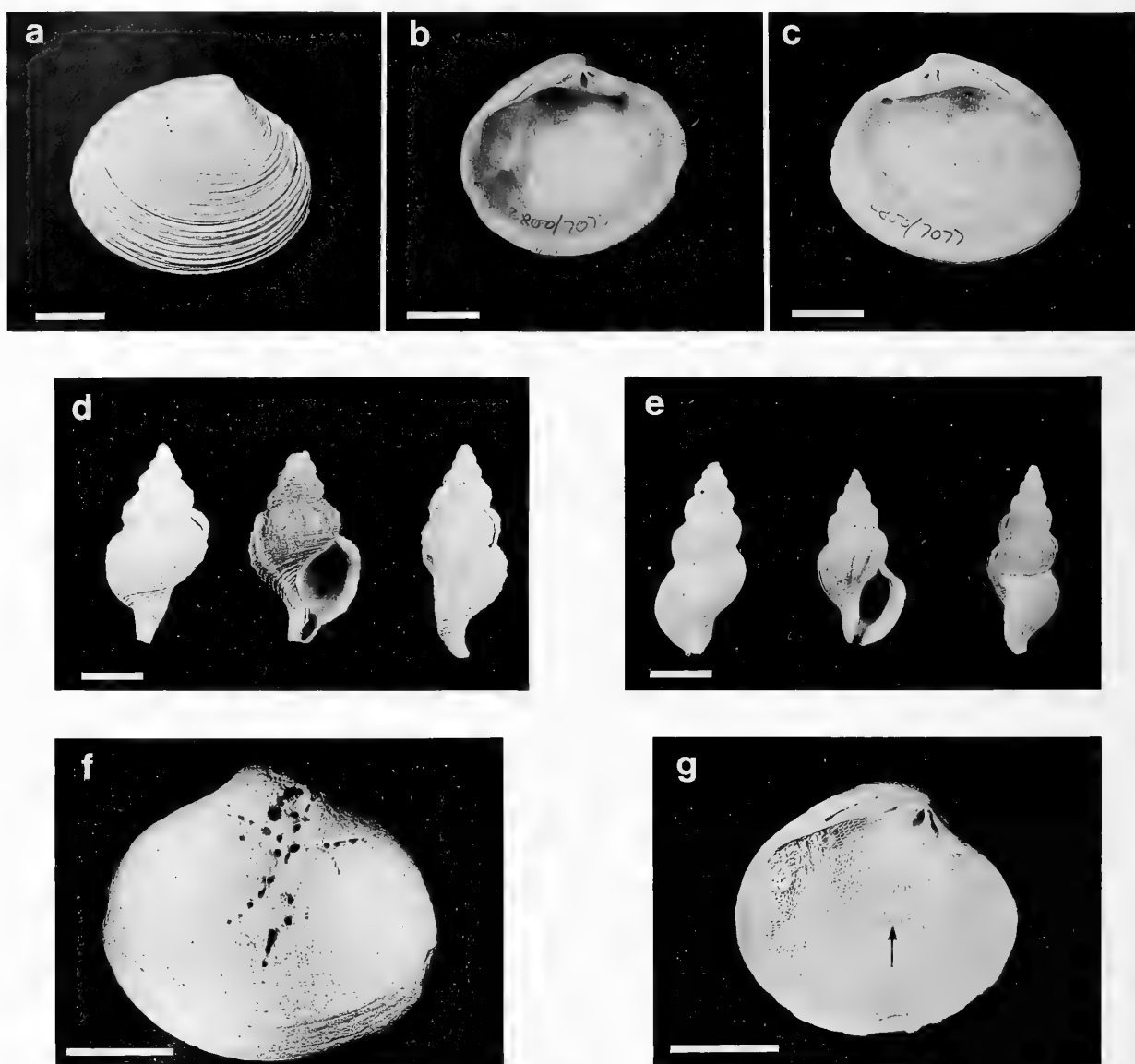


Figure 2

Figure 2a–c. *Tawera philomela*. Figure 2a. Exterior right valve. Figure 2b. Interior left valve. Figure 2c. Interior right valve (SAM-PQ 2681a, b). Figure 2d. *Sassia* (*Sassia*) *philomelae* (SAM-PQ 2682a, b, c). Figure 2e. *Pareuthria fuscata* (SAM-PQ 2683a, b, c). Figure 2f. Abraded exterior of *T. philomela* valve showing unroofed *Entobia* borings (large holes) and *Penetrantia* borings (tiny “pinprick” holes) (SAM-PQ 2684a). Interior of *T. philomela* valve showing *Spathipora* boring (arrowed) and encrusting bryozoans and serpulids (SAM-PQ 2684b). All scale bars are 10 mm. Material deposited in South African Museum.

lections). The very deep record (1800 m) was evidently empty shells (SOOT-RYEN, 1960), and these were probably transported down the steep submarine slopes of Tristan.

Sassia (*Sassia*) *philomelae* (Watson, 1880)

Although this ranellid (Figure 2d) was not present in the bulk shell samples, numerous specimens were collected by De Beers personnel from shell trapped on the gravel screens.

Sassia philomelae is recorded from Nightingale Island, near Tristan da Cunha (WATSON, 1886; BEU, 1985), where it was collected in depths of 180 to 280 m. The genus is not confined to Subantarctic waters and most species occur in the southwest Pacific (Australasia) (BEU, 1985), although the *S. remensa* (Iredale) species group occurs throughout the tropical western Pacific, and *S. nassariformis* (G. B. Sowerby III) occurs off southeast Africa and in the western Indian Ocean.

Pareuthria fuscata (Bruguière, 1789)

A few specimens of this buccinid (Figure 2e) are present in the bulk samples and numerous examples were collected from the screens. The species is recorded from the Strait of Magellan and the Falkland Islands (POWELL, 1954). Material in the South African Museum collected from Gough Island includes this species and represents a new distributional record. SMITH (1885) mentions a record from Kerguelen. The genus is characteristic of Subantarctic and Antarctic waters, and several species are distributed from a center in the Magellanic region eastward to Kerguelen, the Davis and Ross seas, and the Subantarctic islands south of New Zealand (POWELL, 1954). It has been collected from the intertidal to 46 m (SMITH, 1885; POWELL, 1954; South African Museum Collections).

These three species have not previously been recorded from the African coast. However, an assemblage from the Namibian shelf off Sylvia Hill (Figure 1a) contained some shallow-water, relict components (ROGERS, 1977; ROGERS & BREMNER, 1991). A doubtful record in this fauna was *Pitar callicomatus* (Dall, 1902), otherwise known from only a few specimens from tropical west America (KEEN, 1971). Material from off Sylvia Hill, supplied by M. Bremner, confirmed that *Tawera philomela* was present. Misidentification of *T. philomela* seems to have been the source of the erroneous report of *P. callicomatus*.

The extant molluscan fauna of the Namaqua Province on the southwest coast of Africa does contain a Southern Ocean component (e.g., *Choromytilus*, *Aulacomya*, *Argobuccinum*), and it is therefore insufficient to argue that shells of Southern Ocean species are locally extinct because they have been recovered from a relict sediment tract. The input of Subantarctic water into the Benguela Current system is sporadic, but substantial (SHANNON *et al.*, 1989) and the islands of Tristan and Gough straddle the Subtropical Convergence along which this input is sourced. The apparent depth ranges of the species do not preclude them from the depths where collected, except possibly *Pareuthria fuscata*, and an ability to populate a large depth range may be advantageous for species inhabiting the areally limited, shallow shelves of steep oceanic islands. There is no marked contrast in temperature between the islands of Tristan and Gough and the Orange Shelf, and a relict sediment terrain may be the likely habitat of Subantarctic taxa extending their ranges equatorward by submergence. However, additional evidence presented below supports the geologically relict nature of these shells.

EVIDENCE FOR RELICT OCCURRENCE

Shell Taphonomy of *Tawera*

The valves of *Tawera philomela* from the Orange Shelf are abraded to various degrees, bored by endolithic organisms, and encrusted by epilithic taxa. Macroborings represent the ichnogenus *Entobia* Bronn, 1838, which is produced by boring sponges, particularly the Clionidae. The

clionid borings have papillar openings on both sides of the valve, indicating postmortem infestation (BROMLEY, 1970). Smoothed valve exteriors with unroofed *Entobia* are common (Figure 2f) and attest to an abrasive environment. Dissolution was a minor factor, as is evident in the good preservation of *Entobia* wall microsculpture and unetched, well-preserved valve interiors.

The largest microborings are visible to the eye as "pin-pricks" and are always most densely concentrated on the valve exteriors (Figure 2f). Abraded valve surfaces and PVB casts reveal connecting stolons between pits, confirming their bryozoan origin and a morphology attributable to *Penetrantia* Silen, 1946. Another boring bryozoan, *Spathipora* Fischer, 1866, almost exclusively colonized valve interiors (Figure 2g). Several species of unilaminar, cheilostome bryozoans occur in valve interiors, with very few exterior occurrences. Similarly, encrusting serpulid polychaetes, mainly *Spirorbis* spp., occur in valve interiors (Figure 2g). No *Tawera* valves with preserved ligamental material were observed. Fresh *T. philomela* valve interiors have an orange hue. This color is not preserved or is very faint in most Orange Shelf specimens, and specimens with the best color retention are still faded in comparison with fresh specimens from Gough Island.

The PVB casts reveal dense "mats" of microboring between the larger sponge and bryozoan borings and these "mats" are best developed in valve exteriors. This microboring is attributable to endolithic algae and fungi, but the relatively large size of most of the borings (~25 μ m diameter) suggests an algal origin.

Interpretation: Clionid borings occur in both shallow and deep settings and indicate conditions of low sedimentation (EKDALE *et al.*, 1984), but a rich assemblage of sponge borings indicates a depth less than 100 m (BROMLEY, 1970). NELSON *et al.* (1988) have produced a simplified classification of bryozoan growth forms to facilitate their application to palaeoenvironmental studies. Unilaminar encrusting forms, such as those present within *Tawera* shells, are typical of moderate to high current energy and low sedimentation rates, and are most common at inner-shelf depths. The sedentary polychaetes *Spirorbis* spp. are dominantly intertidal to shallow shelf (DAY, 1967).

Notably, *Penetrantia* preferentially infested valve exteriors, while *Spathipora*, spirorbids, and encrusting bryozoans are almost invariably situated in the interior of the valves. This marked partitioning of the concavo-convex shell substratum suggests that most *Tawera* shells were exhumed after death by physical reworking of the sediment and deposited in convex-up, hydrodynamically stable orientations. A similar phenomenon has been documented in detail from bivalves of the Plio-Pleistocene Red Crag by BISHOP (1988), who concluded that the encrusting bryozoan *Cribrilina* exploited the concavities of convex-up shells as a refuge in high-energy environments, the larval settlement behavior apparently being specialized for concavo-convex bivalve substrata. In contrast, valves on the deeper

shelf most often lie in a concave-up position due to the absence of strong currents and activity of carnivores, scavengers, and bioturbation (EMERY, 1968).

The distinction of endolithic algal microborings from borings made by light-independent fungi is difficult due to size and morphological overlap (GOLUBIC *et al.*, 1975). However, in a complex substratum with dark and illuminated surfaces, their distributions will be characteristically different (EKDALE *et al.*, 1984). The fact that the microboring is intensely developed in the exteriors of *Tawera* valves is consistent with an algal origin. PERKINS & HALSEY (1971), examining shells from relict Carolina shelf sediments, found the zone of high algal boring activity to extend to a depth of ~25 m. Two parallel zones located offshore with high incidence of algal boring were interpreted as relict Pleistocene sediments. In clear tropical waters endolithic algae are concentrated shallower than 30 m (ROONEY & PERKINS, 1972; PERKINS & TSENTAS, 1976). Thus, although microboring algae may occur to the limits of light penetration (200–250 m in very clear water), an ichnocoenose that includes abundant algal boring is a useful indicator of inner-shelf palaeodepths.

The abraded, bleached, and bioeroded condition of *Tawera* shells contrasts strikingly with the condition of bivalves in the same samples that are expected to occur in the sample area at present. The valves of *Tellina gilchristi*, *Lucinoma capensis*, and *Dosinia lupinus* are much better preserved, some have vestigial ligamental material, and the relatively few examples that have been subjected to degradation from exposure at the seabed show dissolution effects rather than abrasion. Encrusting and endolithic bryozoa are absent, suggesting that they are characteristic of shallow water in this shelf region. Significantly, microboring is on a finer scale than by *Tawera* (borings 3–4 μm diameter) and numerous spherical sporangial bodies are present, indicative of a fungal origin (PERKINS & HALSEY, 1971; ROONEY & PERKINS, 1972; PEEBLES & LEWIS, 1988). BROWN & HENRY (1985) record the depth of the 1% light level in the southern Benguela region as being from 20 to 30 m, with penetration to 40 m in newly upwelled, phytoplankton-poor water. Doubling of this penetration to compensate for sea-level change is still ~40 m short of the shallowest samples. Thus the probability of the expected Holocene species having been exposed to significant light levels is very low, supporting the fungal origin of their microboring facies. The contrast in microboring facies between *Tawera* and expected Holocene species further supports a mainly algal origin for the microboring in the former.

In summary, the abraded state and the identity and distributions of epi- and endolithic taxa in *Tawera* valves records their exposure on the sea floor as a shelly gravel subjected to current activity within the photic zone. An inner-shelf palaeoenvironment is inferred and indicates that the occurrence of *T. philomela* is relict from a period when shallow water pertained over the sample area. However, the good preservation of the taphonomic features

formed at inner-shelf depths, as well as the occurrence of a minority of very well-preserved valves, indicates that most valves were buried and “stored” in shallow-water sediments. Because the stringent definition of relict occurrence refers to material (sediments and shells), exposed on the seabed, which is “out of place” in the modern environment, these buried shells are not, for the most part, strictly relict. However, a minor portion of abraded, bored *Tawera* valves have superimposed the dissolution and microboring features found on deep-water taxa. These valves indicate continued exposure at the sediment surface as depths increased over the sample area and apparently resided on the top of the bed of shallow-water sediments. This superimposition of the deep-water taphofacies identifies the particular valves that remained on the sediment surface as relict shells for some time.

Sediment Cores

Stratigraphic confirmation of the taphonomic observations was provided by the subsequent recovery of vibracores of sediments from the sample area. These revealed that the postglacial sedimentary sequence in the sample area is condensed due to low sedimentation rates. The *Tawera* valves occur in a gravelly, coarse, polished sand along with worn mytilid and barnacle fragments. *Tawera* valves at the top of the unit have the deep-water taphofacies superimposed. This shallow-water unit, ~0.15 to 0.6 m thick, is overlain by sandy, glauconite-bearing, green mud, varying in thickness from ~0.2 to 1.0 m, which encloses the modern taxa of the area. The *Tawera*-bearing, coarse sand likely continues landward as a transgressive sand sheet beneath the overlying mud, which thickens landward into the Holocene mudbelt lens (ROGERS, 1977).

Dating

A radiocarbon date (Pta-5069) of $13,530 \pm 230$ ^{14}C yr B.P. (400 yr subtracted for the age of seawater) was obtained from particularly well-preserved shells of *Tawera philomela* from ~130 m depth in the sample area (J. C. Vogel, personal communication). The sea-level record obtained from dated corals off Barbados (FAIRBANKS, 1989) indicates an early deglacial sea level at ~100 m at this time. This supports the suggestion that the *Tawera*-bearing coarse sands are inner-shelf deposits, rather than shoreface deposits, and these shallow-shelf sands were rapidly abandoned during the subsequent sea-level surge of the initial, major melt-water episode centered at ~12 ^{14}C kyr B.P. (FAIRBANKS, 1989).

This date may be compared with the 15–11 ^{14}C kyr B.P. spread of dates on cold-water taxa equatorward of the modern ranges on the North American Atlantic shelf (EMERY *et al.*, 1988) and the late glacial 12–13.5 ^{14}C kyr B.P. cluster of ages of “Boreal Guests” from the southern European Atlantic shelf (TAVIANI *et al.*, 1991). Another venerid found equatorward of its modern range in late glacial deposits is recorded from the Mauritanian shelf.

This is *Venus striatula*, dated between 13 and 15 ^{14}C kyr B.P., and suggested to correlate with a stronger, southward-shifted, cold Canary Current (PARK & FÜTTERER, 1989).

The Subantarctic Gastropods

Although examples of *Pareuthria fuscata* and *Sassia philomelae* were poorly represented and absent, respectively, in the shell bulk samples, the fact that they are locally abundant at certain dredge sites (M. Mittelmeyer, personal communication) suggests that local factors of sedimentary history and facies preservation have determined their occurrence. This may result from the *a priori* influence of different environmental preferences of the species. By implication, their taphonomic signature may differ from that of a shallowly infaunal bivalve populating the coarse, periodically mobile, inner-shelf substratum. Because the majority of the available specimens were hand selected from the screens, rather than obtained arbitrarily by bulk sampling, there may also be a bias in observations on their taphonomic state. Nevertheless, it is significant that although relatively few specimens of *Pareuthria fuscata* are abraded, they resemble *Tawera* in that many were densely infested by *Penetrantia* and some contain encrusting bryozoa and spirorbids within apertures. Together with their evidently shallow-water environmental preference, this would suggest penecontemporaneity with *Tawera*. In contrast, the shells of *Sassia philomelae* are not abraded and only a minority were lightly infested by *Penetrantia*, but all are bleached, all show corrosion effects, and most exhibit a pattern of biogenically mediated shell loss resembling that found on expected, deep-water Holocene taxa. Exhumation under deep-water conditions by bioturbation cannot account for this condition, as a preceding, shallow-water taphonomic signature is lacking and the exhumation of practically all specimens is very improbable. This species may have arrived on the African coast at a later time than *Tawera* and *Pareuthria*, or it persisted on the deepening shelf for a considerable time. The last is preferred as the more parsimonious alternative, the condition of *S. philomelae* being due to a greater depth preference than the other Subantarctic representatives, leading to a taphonomic signature characteristic of taxa higher in the faunal succession of the sample area. Additional radiocarbon dating would shed more light on this aspect. The possibility that *S. philomelae* is an undiscovered inhabitant of the deeper shelf off southwestern Africa cannot be excluded.

DISCUSSION

Presuming that *Tawera philomela* larvae drifted to the southern African west coast from Tristan da Cunha and/or Gough islands, the factors facilitating this ~2900 km journey must be considered. A drift card released in the vicinity of Tristan da Cunha took six months to traverse the distance to the Cape coast at a rate calculated at 17 cm/sec (SHANNON *et al.*, 1973). Mean surface drift rates

for cards and buoys between latitudes 30° to 40°S are less, varying from 10 to 15.5 cm/sec, while in the "Roaring Forties" rates of 15 to 20 cm/sec apply (LUTJEHARMS *et al.*, 1988). The absence of modern *T. philomela* on the southern African coast suggests that its larval stage is too short relative to prevailing drift rates to reach Africa.

Sea-surface palaeotemperature estimates for the Last Glacial (~18 kyr B.P.) South Atlantic, based on radiolarians, indicate that Subantarctic waters were 2–5°C colder than today and Subantarctic isotherms were compressed due to a northward shift of the Polar Front toward an essentially stable Subtropical Convergence (MORLEY & HAYS, 1979). This would have resulted in intensification of the atmospheric and ocean circulation, with cooler waters being pumped northward through the Benguela region (MORLEY & HAYS, 1979). NEWELL *et al.* (1981) estimated that the general increase in the intensity of the Last Glacial circulation of the Southern Hemisphere was about 17%. If applicable to the Westerlies, this is insufficient to shorten dramatically drift times from the mid-Atlantic to Africa.

It is possible that the dispersal distance may have been interrupted by colonization of seamount summits (Figure 1c), which would have been shallower during the Last Glacial. Seamounts McNish (–150 m) and RSA (–214 m), although shallow, are too close to the source area to make an appreciable difference. Excessive depth renders the Walvis Ridge an unlikely route. Drift times to Vema (an island during the Last Glacial) may be shorter than to the African mainland, but larvae shed from there are more likely to drift north with the South Atlantic gyre than east toward the mainland. Colonization of Discovery (–329 m), at ~–200 m depth at maximum sea-level fall and probably within the depth range of *Tawera*, would have shortened the traverse by about a third and this southerly route has the advantage of faster drift rates. A role for seamounts, perhaps Discovery, cannot be discounted, but would ultimately require confirmation from the recovery of shells.

Significantly, eight of the ten bivalve species known from Tristan da Cunha have brood protection (SOOT-RYEN, 1960). As remarked by SOOT-RYEN (1960), this is the safest means of propagation on an isolated island, because pelagic larvae would be carried away by currents before ready for bottom life. The maintenance of the population of *Tawera philomela* on the islands seemingly implies a short larval life. On the other hand, the prodissoconch is relatively large (up to 3 mm in height), and the distribution of *Tawera* species attests to successful long-distance dispersal on the geological time scale. Low temperatures and insufficient food are known to slow larval growth. For instance, the pelagic stage of *Mytilus edulis* is potentially more than doubled under these unfavorable conditions (LANE *et al.*, 1985). Furthermore, the pediveliger can delay metamorphosis for up to six weeks in the absence of settlement surfaces (BAYNE, 1965). The species is also able to enter a second, post-larval pelagic stage by byssus rafting, and this ability is reported to be of widespread occurrence in

bivalves, including a venerid (SIGURDSSON *et al.*, 1976). The phenomenon has been examined in detail in *Mytilus edulis*, for which LANE *et al.* (1985) conclude that the potential pelagic existence could exceed six months.

Without specific knowledge of the larval development of *Tawera philomela*, constraints within which to view its dispersal to Africa are lacking. If the larval stage lacks capabilities for prolonged drifting, a significant increase in glacial drift rates is required, or one must resort to the eventual possibility, in geological time, of a "sweepstakes" dispersal event such as the transport of juveniles nestled in the holdfasts of storm-dislodged kelp. The problem of dispersal may not equally apply to *Sassia philomelae*, because tonnageans have teleplanic larvae that can postpone metamorphosis for periods exceeding six months (SCHELEMA, 1971). However, not all tonnageans have equal ability in this regard and the restriction of *S. philomelae* to Tristan da Cunha and Gough islands suggests a short larval life. The dispersal problem is more acute for *Parreuthria fuscata* if, as with most buccinids, they hatch as crawling young from egg cases. This would suggest that the dispersal of *P. fuscata* must have been by way of rafting on flotsam, for instance on kelp fronds. Because sexes are separate, isolated incidences of rafting of individuals are unlikely to result in the establishment of large populations. Another means of rafting is provided by drift pumice from submarine volcanic eruptions (JOKIEL, 1990). Large mats of pumice are produced from mid-ocean volcanic ridges. A submarine eruption near Tristan produced a pumice mat, observed in 1725, that was 480 by 80 km in extent (FRICK & KENT, 1984). It is possible that larvae would settle on such material, with some ultimately making land-fall on the African coast.

A further incidence of long-distance dispersal is the occurrence of shells of the thaidid gastropod *Concholepas concholepas* in Holocene beach sediments in Namibia, just north of the Orange River (Figure 1a) (KENSLEY, 1985). The species is known from the Pliocene to Recent on the Peruvian and Chilean coasts of South America. The Namibian *C. concholepas* may be a chance pioneer population (KENSLEY, 1985), but additional specimens have recently been found much further south near the Olifants River (Figure 1a), in sediments infilling littoral gullies. Both finds may represent isolated populations from chance recruitment, but possibly were dispersed penecontemporaneously during the same unusual conditions. Although the larval life of *Concholepas* exceeds two months (GALLARDO, 1979), drift times to Africa for cards released in the western South Atlantic are ~21 months (SHANNON *et al.*, 1973). Rafting of several individuals, and possibly involving more than one incidence, may account for the occurrences of *Concholepas* on the southwestern African coast. The possibility also exists that the species may have temporarily colonized the Falklands and mid-Atlantic islands.

The wide distributions of many Southern Ocean mollusks is due to the effectiveness of the circumpolar West Wind Drift for dispersal (DELL, 1963; POWELL, 1965;

BEU, 1976). In support of the importance of rafting, POWELL (1965) noted that species associated with algae are particularly well distributed. BEU (1976) suggested that colder sea temperatures during glaciations were instrumental in prolonging the larval lives of several tonnageans, enabling their Southern Ocean dispersal to New Zealand in Pleistocene times. The Last Glacial recruitment of Subantarctic mollusks to the African shelf, from mid-Atlantic islands straddling the Subtropical Convergence, accords with enhanced dispersal opportunities resulting from intensified Westerlies. Glacial conditions in the Southern Ocean apparently enhance dispersal opportunities by increasing the probability that chance "sweepstake" events are successful. Thus the lack of continental shelf areas extending from Africa to high latitudes is compensated to some extent by the glacial cooling and intensification of the circulation. However, for *Tawera* the colonization of the southern African shelf has been only a temporary advance in the circumpolar traverse of the genus back to its Australasian region of origin.

At the Last Glacial Maximum ~18 kyr B.P., cooling of 3–5°C is indicated by radiolaria from a core taken offshore in the northern Benguela (RC13-229, Figure 1a) (MORLEY & HAYS, 1979). This cooling is ascribed to both increased input of cooler waters from the south and increased upwelling stemming from intensification of the circulation (MORLEY & HAYS, 1979; EMBLEY & MORLEY, 1980). However, the presence of the Subantarctic mollusks does not corroborate colder palaeotemperatures for the inshore glacial Benguela environment. Sea-surface temperatures off Tristan da Cunha vary from ~17°C in summer to ~13°C in winter, while waters off Gough Island are 3–4°C colder (ROSCOE, 1979). Inshore temperatures in the Benguela region off northern Namaqualand are thus similar to those off Tristan, with more local cooling due to upwelling producing temperatures similar to those off Gough in winter (9–10°C) (SHANNON, 1985). Upwelling in the southern Benguela region is strongly modulated (subdued) by the passage of frontal systems embedded in the Westerlies south of Africa (SHANNON, 1985), but there are no data to examine the possibility of decreased upwelling associated with the intensified glacial Westerlies. Stable isotope ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) and trace element profiles from incremental sampling of Recent and fossil bivalve shells have been shown to be a record of shelf temperatures, their seasonality, and hydrographic events such as upwelling (KRANTZ *et al.*, 1987; KRANTZ, 1990). An inner-shelf, shallow-infaunal venerid such as *Tawera* may be a suitable candidate for such studies, with dated and analyzed shells providing "snapshots" of the late Quaternary Benguela inner-shelf environment.

The timing of the arrival of the Subantarctic mollusks, the latitudinal range successfully colonized along the African coast, and when they became locally extinct, are outstanding questions. Evidence for arrival during the regression leading up to the Last Glacial maximum of sea-level fall might not be preserved due to erosion as the

regression continued and subsequent erosion during the deglacial transgression. Indications of the timing of their local extinction is beneath the Holocene muds landward of the relict sediment terrain, where their disappearance from the transgressive sand sheet would indicate their demise. It is possible that warm-water events approximately 13 and 10 kyr B.P., evidenced by dated Algoa-Natal mollusks from the sample area (in preparation), might have contributed to their extinction. Another possibility is that the oxygen-poor, sulphide-rich benthic environment beneath the modern upwelling regime was unfavorable. One may speculate that *Concholepas concholepas* was also recruited during glacial times, but persisted during the deglacial transgression, only becoming extinct during high Holocene temperatures. However, its shells have yet to be found in the sediments relict from the Last Glacial shoreline and the deglacial transgression.

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The Gastropods in the Streams and Rivers of Four Islands (Guadalcanal, Makira, Malaita, and New Georgia) in the Solomon Islands

by

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Abstract. Several streams and rivers on the Solomon Islands of New Georgia, Guadalcanal, Makira, and Malaita were surveyed for gastropods in 1987 and 1988. Altogether 33 species of freshwater gastropods were collected—22 species from New Georgia, 19 from Guadalcanal, 19 from Makira, and 16 from Malaita. The rivers with low ion content (conductivity $181 \mu\text{S cm}^{-1}$) on the totally volcanic island of New Georgia had as many gastropod species as did those with high ion content (conductivity $234\text{--}374 \mu\text{S cm}^{-1}$) on the partially limestone islands of Guadalcanal, Makira, and Malaita. All species belonged to the prosobranch families Neritidae and Thiariidae.

INTRODUCTION

Several collections of freshwater gastropods were made from New Guinea and Solomon Islands during the nineteenth century. Most of these collections were examined and described by RIECH (1937). STARMÜHLNER (1976) collected freshwater gastropods from the island of Guadalcanal and I (HAYNES, 1990) briefly described my collection for New Georgia.

The Pacific island country of Solomon Islands is composed of six major island groups. These are Choiseul, Santa Isabel, Malaita, New Georgia, Guadalcanal, and Makira (San Cristobal) (Figure 1). The islands lie just south of the equator and as a result the climate is hot and humid throughout the year.

The major islands are steep and large areas are still covered in forest. As a result many of the rivers and streams are not readily accessible even though the islands are easily reached by boat or plane.

Gastropods mentioned in this report were collected from two streams on New Georgia in 1987 and from Guadalcanal, Makira, and Malaita in 1988. This enabled a comparison of the gastropod fauna of two types of island groups, one group overlaid with limestone rock (Guadalcanal, Makira, and Malaita), the other (New Georgia) lacking a limestone overlay.

STUDY AREA

The geographical positions of the four islands investigated are shown in Figure 1.

Geologically, Guadalcanal, Makira, and Malaita are similar. All have a basement of upper Mesozoic lavas overlain by sedimentary rocks, mainly chalky carbonate sediments. The New Georgia group on the other hand is composed of upper Miocene to Recent andesitic volcanic cones, lagoons, and fringing reefs (HACKMAN, 1973).

Guadalcanal is the largest island in the Solomon Islands with an area of 5336 km^2 and a maximum height of 2447 m. It and Malaita are the only islands with any length of road. All sampling sites (sites 4–9) on Guadalcanal were on the more accessible northern coast (Figure 1). Malaita, the second largest island, has an area of 4243 km^2 and a height of 1303 m. Here the streams and rivers visited (sites 16–21) were in North Malaita, near Auki or on the Atori road (Figure 1). Malaita is the most densely populated of the four islands. Makira, area 3188 km^2 and height 1250 m, is mostly inaccessible by road. Sampling was carried out on the north coast (sites 10–15) near Kirikiri, the Provincial administrative center (Figure 1). The island of New Georgia is part of the Western Province. It is a forest-clad island with wide lagoons. Most villages have been built on the lagoons. The Puha River (sites 1–2) flows into

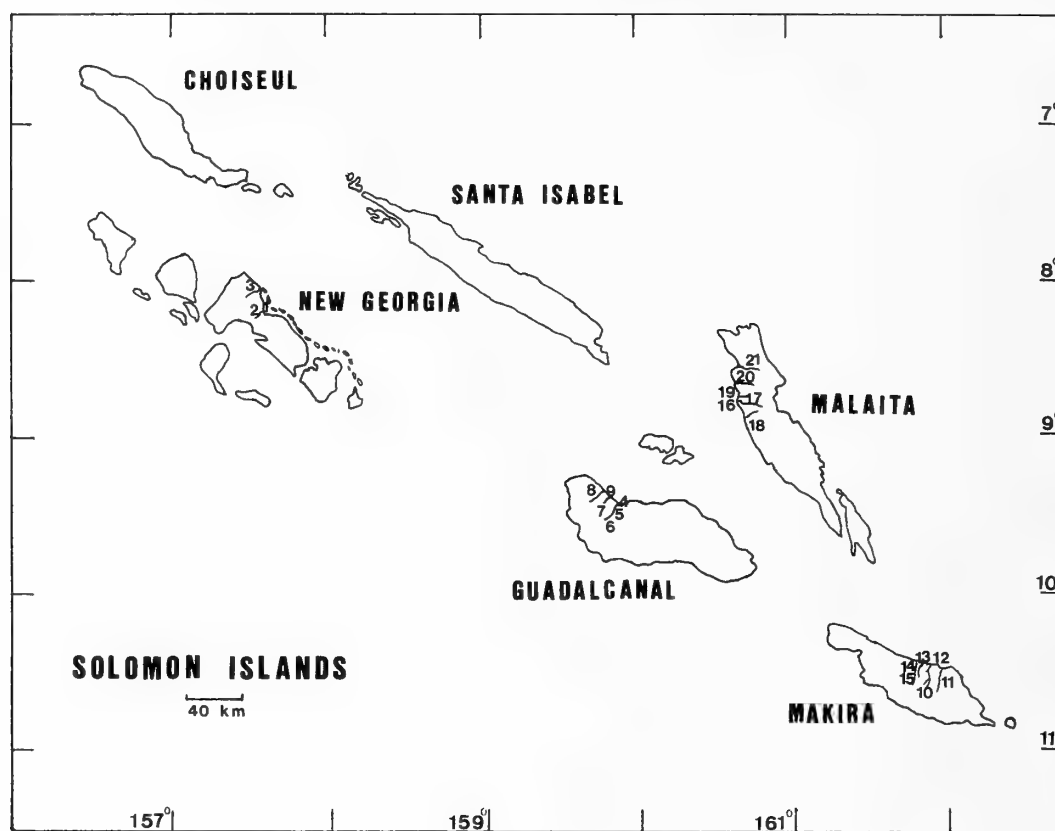


Figure 1

A map of the main Solomon Islands showing the localities of the sampling stations on New Georgia, Guadalcanal, Makira, and Malaita.

the Kaisi end of the Marovo Lagoon and can only be reached by boat. The Borora River (site 3) is near the abandoned logging town and air strip at Borora (Figure 1).

Several of the rivers on Guadalcanal and Makira were carrying a heavy load of sediment washed from the hill-sides, where the forest was being logged.

MATERIALS AND METHODS

Sampling took place on New Georgia in July 1987 and on Guadalcanal, Makira, and Malaita from 26 August to 6 September 1988, with the exception of site 9 (ICLARM), which was sampled in July 1990 (Figure 1).

The substratum at each station was searched for gastropods for at least 30 min. The leaf litter, plants, wood, and all surfaces of stones and boulders were inspected and the sand and gravel were sieved. The specimens collected in this way were killed in magnesium sulphate solution and then preserved in 80% ethanol for later identification.

The substratum, pH, water speed, and temperature were noted and water samples were collected at some stations. These were analyzed for total ions (conductivity $\mu\text{S cm}^{-1}$) and hardness (mg CaCO_3/L) by the Institute of Natural Resources, University of the South Pacific (Table 1).

RESULTS

Altogether 33 species of gastropods were collected from the Solomon Islands streams and rivers—22 from New Georgia, 19 from Guadalcanal, 19 from Makira, and 16 from Malaita (Table 1). Collecting difficulties, due to constant rain and swollen rivers, encountered on Malaita may account for the smaller number of species found there.

All gastropods collected belonged to the families Neritidae and Thiaridae. Voucher specimens of the species collected were deposited in the Australian Museum, Sydney, Australia, and duplicate specimens are available at the School of Pure and Applied Sciences, University of the South Pacific, Suva, Fiji. The 22 species of Neritidae found were *Clithon adumorata* (Reeve) (C172785), *Clithon chlorostoma* (Sowerby) (C172786), *Clithon corona* (Linné) (C172787), *Clithon nucleolus* (Morelet) (C172788), *Clithon olivaceus* (Récluz) (C172789), *Clithon oualaniensis* (Lesson) (C172790), *Clithon squarrosus* (Récluz) (C172791), *Clithon waigiensis* (Lesson) (C172792), *Neritina asperulata* Récluz (C172793), *Neritina auriculata* Lamarck (C172794), *Neritina canalis* Sowerby (C172795), *Neritina macgillivrayi* Reeve (C172796), *Neritina petiti* Récluz (C172797), *Neritina pulligera* (Linné) (C172798),

Table 1

The physical conditions, results of water analysis, and gastropods present at the sampling stations on the islands of New Georgia, Guadalcanal, Makira, and Malaita.

Station	River and map ref.	River width (m)	Distance from sea	Main substratum	Water speed (cm sec ⁻¹)	Temperature (°C)	Total ions (μS cm ⁻¹)	Hardness (mg CaCO ₃ /L)	pH	Gastropods present
New Georgia										
1	Puha R. 8°11'S, 157°37'E	10	10–40 m	stones, boulders	10–20	26	—	—	—	<i>Clithon chlorostoma</i> , <i>C. corona</i> , <i>C. nucleolus</i> , <i>C. waigiensis</i> , <i>Neritina asperulata</i> , <i>N. auriculata</i> , <i>N. canalis</i> , <i>N. squamipicta</i> , <i>Septaria tessellata</i> , <i>S. porcellana</i> .
2	Puha R. 8°11'S, 157°37'E	6	1 km	boulders, rocks	50–80	25	181	21.5	6.9	<i>Clithon nucleolus</i> , <i>C. squarrosus</i> , <i>C. waigiensis</i> , <i>Neritina asperulata</i> , <i>N. canalis</i> , <i>N. petiti</i> , <i>N. pulligera</i> , <i>N. macgillivrayi</i> , <i>N. squamipicta</i> , <i>N. variegata</i> , <i>Neritodryas cornea</i> , <i>N. subsulcata</i> , <i>Septaria porcellana</i> , <i>S. sanguisuga</i> , <i>Melanoides aspirans</i> , <i>M. punctata</i> , <i>Thiara cancellata</i> .
3	Borora R. 8°02'S, 157°35'E	7	50 m	stones	20–30	26	—	—	—	<i>Clithon nucleolus</i> , <i>Melanoides tuberculata</i> , <i>M. aspirans</i> , <i>M. cancellata</i> , <i>Neritina petiti</i> , <i>N. pulligera</i> , <i>N. variegata</i> , <i>Septaria porcellana</i> .
Guadalcanal										
4	Botanical gardens stream 9°23'S, 159°55'E	5	50 m	stones, boulders	20–30	28	—	—	—	<i>Clithon oualaniensis</i> , <i>C. nucleolus</i> , <i>C. squarrosus</i> , <i>Septaria porcellana</i> , <i>Thiara scabra</i> .
5	Botanical gardens stream 9°23'S, 159°55'E	8	0.5 km	stones	30–40	28	374	176.51	7.5	<i>Melanoides aspirans</i> , <i>M. punctata</i> , <i>Neritina canalis</i> , <i>N. variegata</i> , <i>Thiara scabra</i> , <i>Tarebia granifera</i> .
6	Botanical gardens stream 9°23'S, 159°55'E	8	1.5 km	stones, boulders	30–50	27	—	—	—	<i>Balanocochlis glans</i> , <i>Clithon adumbrata</i> , <i>Melanoides punctata</i> , <i>Neritina canalis</i> , <i>N. variegata</i> , <i>Melanoides arthurii</i> , <i>Thiara bellicosa</i> , <i>T. scabra</i> .
7	Mamara R. 9°22'S, 159°54'E	5	100 m	gravel	0–20	29.5	309	135.13	7.05	<i>Clithon corona</i> , <i>C. nucleolus</i> , <i>Neritina squamipicta</i> , <i>Septaria porcellana</i> , <i>Tarebia granifera</i> .
8	Bonehe R. 9°21'S, 159°52'E	15	1.5 km	stones	30–50	27.5	—	—	—	<i>Clithon adumbrata</i> , <i>C. squarrosus</i> , <i>C. nucleolus</i> , <i>Melanoides tuberculata</i> , <i>M. aspirans</i> , <i>M. pallens</i> , <i>Neritina squamipicta</i> , <i>Septaria porcellana</i> , <i>Tarebia granifera</i> .
9	ICLARM 9°22'S, 159°53'E	6	10–40 m	stones, gravel	0–20	27	—	—	—	<i>Clithon chlorostoma</i> , <i>C. nucleolus</i> , <i>Melanoides tuberculata</i> , <i>Neritina canalis</i> , <i>N. squamipicta</i> , <i>N. variegata</i> , <i>Thiara granifera</i> , <i>T. bellicosa</i> , <i>Septaria porcellana</i> .
Makira										
10	Towitara R. 10°27'S, 161°56'E	5	10–100 m	stones	10–30	25	234	103.84	7.7	<i>Clithon nucleolus</i> , <i>Melanoides punctata</i> , <i>Neritina auriculata</i> , <i>N. asperulata</i> , <i>N. variegata</i> , <i>Septaria porcellana</i> , <i>N. violacea</i> .
11	Ravo R. 10°29'S 161°58'E	16	1 km	stones	20–50	26	—	—	—	<i>Melanoides pallens</i> , <i>Neritina pulligera</i> , <i>N. variegata</i> , <i>Septaria porcellana</i> , <i>Thiara granifera</i> .

Table 1
Continued.

Sta- tion	River and map ref.	River width (m)	Distance from sea	Main substratum	Water speed (cm sec ⁻¹)	Tem- pera- ture (°C)	To- tal ions (μS cm ⁻¹)	Hard- ness (mg CaCO ₃ / L)	pH	Gastropods present
12	Arohane stream 10°28'S, 161°57'E	4	500 m	stones	20-40	26	—	—	—	<i>Balanocochlis glans</i> , <i>Clithon adumorata</i> , <i>Melanoides pallens</i> , <i>M. plicaria</i> , <i>Neritina canalis</i> , <i>N. pulligera</i> , <i>N. variegata</i> .
13	Kirikiri R. 10°27'S, 161°55'E	8	500 m	basalt and limestone stones	30-40	26	273	121.18	7.4	<i>Balanocochlis glans</i> , <i>Clithon nucleolus</i> , <i>C. olivaceus</i> , <i>Melanoides aspirans</i> , <i>M. pallens</i> , <i>M. plicaria</i> , <i>M. punctata</i> , <i>Neritina variegata</i> , <i>N. pulligera</i> , <i>Septaria porcellana</i> .
14	Huro R. 10°27'S, 161°54'E	8	10-50 m	stones	30-40	27	—	—	—	<i>Clithon corona</i> , <i>C. nucleolus</i> , <i>C. wai-giensis</i> , <i>Melanoides pallens</i> , <i>M. punctata</i> , <i>Neritina pulligera</i> .
15	Huro R. 10°27'S, 161°54'E	10	1.0 km	stones	40-50	26	—	—	—	<i>Balanocochlis glans</i> , <i>Clithon corona</i> , <i>C. nucleolus</i> , <i>C. olivaceus</i> , <i>Melanoides aspirans</i> , <i>M. pallens</i> , <i>M. punctata</i> , <i>M. plicaria</i> , <i>Neritina asperulata</i> , <i>N. pulligera</i> , <i>N. variegata</i> , <i>Septaria porcellana</i> , <i>N. squamipicta</i> .
Malaita										
16	Kwaibola R. 8°46'S, 160°42'E	10	400 m	stones, limestones	30-40	27	—	—	—	<i>Clithon nucleolus</i> , <i>C. squarrosus</i> , <i>C. wai-giensis</i> , <i>Melanoides pallens</i> , <i>Neritina auriculata</i> .
17	Kwaibola R. 8°46'S, 160°42'E	12	1.0 km	stones, limestones	30-60	26	288	141.89	7.5	<i>Clithon chlorostoma</i> , <i>C. squarrosus</i> , <i>Melanoides pallens</i> , <i>Neritina auriculata</i> .
18	Ura R. 8°49'S, 160°44'E	10	1.5 km	stones	30-40	26	—	—	—	<i>Clithon corona</i> , <i>Melanoides pallens</i> , <i>M. punctata</i> , <i>Septaria porcellana</i> .
19	Kwaiofoa R. 8°42'S, 160°42'E	15	1.0 km	stones (in flood)	50-80	26	—	—	—	<i>Melanoides arthurii</i> , <i>Thiara scabra</i> .
20	Banio R. 8°36'S, 160°41'E	8	3.0 km	stones, gravel, limestones	40-50	26	—	—	—	<i>Clithon adumorata</i> , <i>Melanoides pallens</i> , <i>M. tuberculata</i> , <i>Neritina macgillivrayi</i> , <i>Tarebia granifera</i> .
21	Kao R. 8°35'S, 160°46'E	5	12 km	boulders, limestone, rocks	30-80	25	257	129.99	7.7	<i>Melanoides pallens</i> , <i>M. tuberculata</i> , <i>Neritina variegata</i> .

Neritina squamipicta Récluz (C172799), *Neritina variegata* (Lesson) (C172800), *Neritina violacea* (Gmelin), *Neritodryas cornea* (Linné) (C172801), *Neritodryas subsulcata* (Sowerby) (C172802), *Septaria porcellana* (Linné) (C172803), *Septaria sanguisuga* (Reeve) (C172804), *Septaria tessellata* (Lamarck) (C172805). The 11 species of Thiariidae were *Balanocochlis glans* (v. d. Busch) (C172806), *Melanoides arthurii* (Brot) (C172807), *Melanoides aspirans* (Hinds) (C172808), *Melanoides pallens* (Reeve) (C172809), *Melanoides plicaria* (Born) (C172810), *Melanoides punctata* (Lamarck) (C172811), *Melanoides tuberculata* (Müller) (C172812), *Tarebia granifera* (Lamarck) (C172813), *Thiara*

bellicosa (Hinds) (C172814), *Thiara cancellata* Röding (C172815), and *Thiara scabra* Müller (C172816).

Clithon nucleolus, and sometimes *C. squarrosus*, were very abundant from the mouth to about 0.5 km upstream in the rivers and streams on Makira and Malaita. The local people on Malaita call them *Korona* and use them as food.

The species mixture on Guadalcanal, Makira, and Malaita was similar, but in the steep fast-flowing Puha River on New Georgia, *Neritina macgillivrayi* was the most abundant species and *Septaria sanguisuga* and *S. tessellata* were present; these species of *Septaria* were not found on other islands (Table 1).

Total ions ($234\text{--}374\ \mu\text{S cm}^{-1}$) and hardness ($103.84\text{--}176.51\ \text{mg CaCO}_3/\text{L}$) were high in the rivers of the partly limestone islands of Guadalcanal, Makira, and Malaita compared with total ions ($181\ \mu\text{S cm}^{-1}$) and hardness ($21.5\ \text{mg CaCO}_3/\text{L}$) in the Puha River on the completely volcanic island of New Georgia (Table 1). However, the total ion content of the water did not appear to influence the number of gastropod species in a stream. Although no quantitative counts were made, observation showed that gastropods were more abundant in streams with high ion content. The shells of some species (e.g., *Melanoides pallens* and *Neritina variegata*) in the streams with high calcium carbonate concentration were often heavily encrusted with limestone.

Many specimens of the genus *Neritodryas* were found in small temporary runnels. Their empty shells were also found in dried-up runnels suggesting that many of them died when the water receded.

DISCUSSION

Gastropods were very abundant in the rivers on the islands of Guadalcanal, Makira, and Malaita with high ion content, but species richness was no greater than on the island of New Georgia. *Melanoides punctata*, *M. pallens*, and *Tarebia granifera* were not found on New Georgia; however, this was probably not due to differences in water chemistry, but because the streams of New Georgia had beds composed of boulders and rocks rather than of stones.

Septaria tessellata and *S. sanguisuga* were found only in the Puha River, New Georgia, although *S. tessellata* has been reported from New Guinea and southeastern Asia. The distribution of *S. sanguisuga* is also widespread. It has been found on islands as far apart as Ponepe in the northern Pacific and Samoa and Fiji in the southwestern Pacific (HAYNES, 1990). *Septaria sanguisuga* and *Neritina macgillivrayi* may be present in the steeper faster streams on the southern sides of Guadalcanal and Makira.

Although only specimens of the families Neritidae and Thiaridae were found on this survey, STARMÜHLNER (1976) collected the opisthobranch *Strubellia paradoxa* in the Matanikau River, Guadalcanal.

The neritid and thiarid gastropods are generally supposed to have originated in southeastern Asia, where most species present in New Guinea and the Solomon Islands are found (RIECH, 1937; STARMÜHLNER, 1976). Two species, *Neritina pulligera* and *N. turrita*, have been found in Pliocene and Pleistocene rocks in east Java (BENTHEM-JUTTING, 1956). Another pointer to a southeast Asian origin to the Solomon Islands thiarids and neritids is the presence of the same species on Indian Ocean islands—e.g., *N. pulligera* and *Clithon chlorostoma* on Seychelles and Comoros (STARMÜHLNER, 1983), *Thiara scabra*, *Melanoides tuberculata* and *N. auriculata* on Mauritius (STARMÜHLNER, 1983), and *Clithon corona*, *N. auriculata*, *N. variegata*, *T. scabra*, *N. pulligera*, *N. squamipicta*, *Ner-*

itilia rubida, *M. tuberculata*, *M. plicaria* and *Tarebia granifera* on the Andaman Islands (STARMÜHLNER, 1984).

Of the 33 species of gastropods found on the Solomon Islands, 20 of them are present on the Fiji islands (HAYNES, 1985, 1988, 1990). Eight species have been reported from the Fiji islands but not from the Solomon Islands. Some species found on the Solomon Islands have not been found as far south as Fiji but are in New Caledonia—e.g., *Septaria porcellana*, *Clithon nucleolus*, and *Neritina asperculata* (STARMÜHLNER, 1970). On the other hand the species *S. bougainvillei*, *S. macrocephala*, and *Physastra nasuta* and the genus *Fluviopupa* are found in Fiji and New Caledonia but not in the Solomon Islands. *Septaria bougainvillei* and *S. macrocephala* probably evolved in the Fiji-New Caledonia region (HAYNES, 1992) while the genera *Physastra* and *Fluviopupa* are of Australian origin (PONDER, 1982; WALKER, 1984; HAYNES, 1990).

The present distribution of neritid and many thiarid freshwater gastropods is thought to have occurred by their veliger larvae being carried by ocean currents from island to island. I have found that *Clithon* and *Neritina* veligers can survive in seawater if acclimatized in a series of dilutions that they are likely to experience at the mouth of rivers (HAYNES, 1990).

The water speed, and consequently the nature of the substratum, and the number of microhabitats are the major factors that determine which species and how many species will be found at any one site in a river. These factors are more important than water chemistry in determining which species of gastropods will inhabit a stream.

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NOTES, INFORMATION & NEWS

Ampullariid Phylogeny—Book Review and Cladistic Re-analysis

by

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A monograph of the gastropod family Ampullariidae was recently published. It presents revised hypotheses of ampullaroidean phylogeny and also addresses more general issues of phylogenetic systematics (the author, for instance, introduces a *Fitness-Prinzip* to polarize character states). An in-depth review of this massive German-language work seems appropriate.

BERTHOLD, Thomas. 1991. Vergleichende Anatomie, Phylogenie und historische Biogeographie der Ampullariidae (Mollusca, Gastropoda). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 29: 256 pp., 358 text-figs. Verlag Paul Parey: Hamburg and Berlin. ISBN 3-490-15196-8; DM 98.00; exact publication date, 12 December 1991 [O. Kraus, editor, in litt.].

The monograph is arranged in three main parts (anatomy, phylogenetic reconstruction, biogeography); a taxonomic appendix is added. The extensive first part (pp. 19–129) contains very detailed descriptions of the shell, external morphology, mantle cavity, circulatory system, alimentary tract, and nervous system, as well as a short section on locomotion. Anatomical studies, within each topic usually arranged by genus, are documented in great detail with numerous line drawings (*e.g.*, of buccal musculature and nervous system), and are supported by light photomicrographs of histological sections (*e.g.*, of the palial oviduct) and SEM photomicrographs (*e.g.*, of the ampulla [a modified section of the anterior aorta], of sperm in testis follicles, and of radulae).

Taxonomic Scope of the Work

On the basis of his anatomical studies of 36 species in 6 genera, the author recognizes as valid genus-group taxa in the Ampullariidae: *Afropomus* Pilsbry & Bequaert, 1927; *Saulea* Gray, 1867; *Lanistes* Montfort, 1810 (with subgenus *Plesiolanistes* Berthold, 1991), *Pseudoceratodes* Wenz, 1928; *Pila* Röding, 1798; *Asolene* d'Orbigny, 1837; *Felipponea* Dall, 1919; *Pomella* Gray, 1847 (with subgenus *Surinamia* Clench, 1933); *Marisa* Gray, 1824; and *Pomacea* Perry, 1810 (with subgenus *Effusa* Jousseaume, 1889). Several previously recognized ampullariid taxa (*Ampul-*

laria, *Ampullarius*, *Ampulloidea*, *Ceratodes*, *Conchylium*, *Kwangispira*, *Leroya*, *Limnopomus*, *Meladomus*, *Pachychilus*, *Pachylabra*, *Pachystoma*, *Pomus*, *Prolanistes*, *Turbini-cola*) are placed in synonymy. Not all of the accepted genus-group taxa are well supported by autapomorphies. *Asolene*, for instance, is characterized as having secondarily gelatinous eggs (a character unknown for some included species), and the only cited autapomorphy for *Plesiolanistes* is the reduction of shell carinae in the west African populations of the single species (p. 210).

The work is not intended to assist identification at the species level. A tally of the number of ampullariid species (pp. 20–25) gives a total of approximately 120, a few of them known from fossils only. The analysis is restricted to a subset of these species, *i.e.*, those for which anatomical material was available to the author. Thirty-two nominal species are illustrated by shell photographs (figs. 1–33), and 36 nominal species are listed in the Material and Methods section (pp. 13–36). For *Lanistes*, all extant species but *L. alexandri* were studied anatomically, and this genus was treated in greater detail. Few references have been included after late 1988, and the current discussion of the phylogenetic position of Architaenioglossa (*Proso-branch Phylogeny* volume [PONDER, 1988, ed.] and subsequent papers) is thus not addressed.

Taxonomic Treatment

Compared to the excellent anatomical part of this work, the taxonomic part has some problems. Some of this is due to technicalities (for instance, the repeatedly mentioned ampullariid genus “*Limnopoma*” [*e.g.*, p. 23 as “*emend.*,” p. 203, and cladograms in part 2] should read *Limnopomus* Dall, 1904). The discussion of the family name Pilidae (a junior synonym of Ampullariidae) is erroneous (p. 245), in that the name was not first introduced by Conolly, 1927, as stated, but by PRESTON, 1915:96.

The family is divided into two subfamilies, monotypic Afropominae Berthold, 1991 (with only one Recent species, *Afropomus balanoides*), and Ampullariinae Perry, 1810. The latter is divided into monotypic Sauleini Berthold, 1991, and Ampullariini. Other previously proposed subunits (such as “*Lanistinae*” of Starobogatov in SITNIKOVA & STAROBOGATOV, 1982) remain undiscussed. In addition to formally introducing three ICZN-regulated names (the two family-group taxa mentioned above and new subgenus *Plesiolanistes*), Berthold introduced names for several groups of ampullariid genera (above genus-, below tribe-level). The decision to name most clades in the preferred cladogram resulted in five new names that have no formal nomenclatural bearing. One name in particular proves to

be an unfortunate choice. Berthold introduced the new name "Heterostropha" for the clade comprising the genera *Lanistes* and *Pseudoceratodes*. However, the identical name (*Heterostropha* Fischer, 1885) is already in use for another much larger "informal" group of Gastropoda (*e.g.*, GOLIKOV & STAROBOGATOV, 1975; PONDER & WARÉN, 1988). More importantly, the phenomenon meant by Berthold in using the name *Heterostropha* is, according to established definitions, not *heterostrophy* but *hyperstrophy*. *Heterostrophy* is defined as divergent coiling directions of proto- and teleoconch, a condition not known in ampullariids (see *e.g.*, LANG, 1900:248, fig. 246; COX, 1960:111, fig. 67).

Methodology

Berthold aims to reconstruct the phylogeny of Ampullariidae, based on his studies of comparative anatomy and "by consistent application of Hennig's method of Phylogenetic Systematics" (cover text). He stresses the importance of integrating data derived from ecology, ontogeny, physiology, and biogeography, to "do justice to both aspects of phylogenesis—that of cladogenesis and anagenesis," and his study attempts "not only to resolve but to explain the phylogenesis of Ampullariidae (p. 8; my translation).

In addition to providing a monograph of the Ampullariidae, the author addresses a variety of topics in biology and philosophy. Some of this occurs in unexpected places; for instance, in the section on the ampullariid nervous system, he introduces the term "Symmetricon" (which the author suggests to replace "symmetrical counterpart" in morphological descriptions). Important issues that should have been discussed in more-developed separate manuscripts (or at least sections) are treated superficially. For instance, "transformed cladism" is mentioned and curtly dismissed, but instead of offering constructive discussion, the author broadly advises the reader to study the journal *Evolution* (p. 130). Similarly shallow treatment is given to "vicariance biogeography" in the introduction to the chapter of biogeography (pp. 213–214). The cited literature base is small; the treatment of adaptation, for instance, is largely restricted to the European body of literature (p. 131).

The second part of the monograph, phylogeny reconstruction (pp. 129–213), begins with a chapter on methodology. Here (pp. 131–133), criteria for polarization and ordering of character states are evaluated. Berthold discusses *Ökonomie-Prinzip*, as suggested by BOCK & WAHLERT (1965) and PETERS & GUTMANN (1971), a poorly known concept in the English-language literature. Dismissing energy consumption as a criterion for character evaluation, Berthold introduces *Fitness-Prinzip*.

According to the author, the *Fitness-Prinzip* "permits the establishment of correlations between adaptational processes and relative fitness as a means of character evaluation" (p. 3). "If a character transformation can be expected to increase fitness—it will in following generations displace, and finally replace, the 'inferior' character state"

(p. 137, my translation). However, Berthold does not refute Ax's criticism (Ax, 1988:85–87) that adaptational value-hypotheses are non-falsifiable. The penguin example (p. 133), presented to illustrate the reasoning within the *Fitness* paradigm, demonstrates that the polarization (of wing structure and function in penguins) is actually based upon outgroup comparison (flight ability presumed plesiomorphic), with an *a posteriori* adaptational "explanation."

The author employs the *Fitness-Prinzip* for various character states in two organ systems, the lung sac (p. 169) and the male copulatory organ (p. 181). In both cases, character transformation from simple to complex is assumed. The alleged adaptational parameters (*e.g.*, improved oxygen acquisition, reduction of sperm loss) are not supported by concrete physiological data. The "fitness" criterion is applied whenever an adaptational hypothesis could be developed. In cases where the *Fitness-Prinzip* appears inapplicable and outgroup comparison cannot help (*e.g.*, presence of shell ridges), the author lets congruence decide among the hand-constructed cladograms. When a hypothesis implies too many convergences, he returns to parsimony decisions ("multiple convergent reductions . . . a much more cumbersome assumption"; p. 161).

In the second part of the monograph, character states are polarized considering "adaptive value" (*Fitness-Prinzip sensu* Berthold) and outgroup relationship. In the section on conchological characters (including periostracum and operculum), the genus *Lanistes* is treated in detail, offering three species-level cladograms in which modifications of shell form or carination pattern are given "highest priority" (figs. 324–326). Others are based on lung-sac characters, alimentary tract, or combinations of several character suites. At the family level, several hand-constructed cladograms are based on character subsets, *e.g.*, shell characters, external morphology and mantle cavity organs, ampulla shape, kidney, and reproductive, alimentary, and nervous systems. The various diagrams of relationship (*Verwandschaftsdiagramme*; figs. 327–331, 335–341, and 343) are considered largely congruent (p. 198). After a reassessment of nominal genera (pp. 199–206), a "preferred hypothesis of ampullariid relationships, based on character evaluation of all characters here discussed" (p. 204; my translation) is offered (*i.e.*, an informal consensus tree of the diagrams presented before).

Phylogenetic Analysis

The phylogenetic part of the work culminates in the presentation of a cladogram of phylogenetic relationships within the Ampullariidae (figs. 348–349), which is stated to be supported by 146 autapomorphies (p. 208). The data are not presented in a formal data matrix, instead the "autapomorphies" are numbered and described in the text (pp. 209–212). One problem with this approach is that the character state distributions in the analysis cannot always be unequivocally reconstructed. Since the author often describes trends ("secondarily heightened, overall still

flat," "reduced," "narrowed") rather than actual states, much information remains subject to interpretation.

The 146 entries in this list are the total of all character state changes, including reversals and parallelisms. Coding is inconsistent; for instance, the (congruent) character state changes "calcareous egg shell" (#84) and "egg deposition outside water" (#85) are coded separately, while the reversals ("eggs secondarily gelatinous and subaquatic" are treated as one change (#120, and also #134). The figure caption to fig. 348 indicates that there are 11 occurrences of convergence in this tree. The text shows there are several more (e.g., "median carina reduced," indicated as convergence for changes #33 and #77 only, also occurs as changes #65 and #75).

Of the 146 listed character state changes, 80 are synapomorphies at the family level or autapomorphies of the terminal taxa, and thus can only be informative for ingroup relationships if they are parts of multi-state character series. There is no formal distinction between binary and multi-state characters, but some of the listed changes are clearly multi-state series (e.g., shell spire shortened [#104], further shortened [#107], extremely shortened [#111]). With no formal data matrix at hand, interpreting Berthold's character state descriptions is sometimes difficult, especially since the wording is inconsistent and differs between parts of the monograph. In table 1 (conchological characters; p. 26), for instance, "inflated" (*aufgebläht*) is the only term for apertural inflation, while the cladogram (fig. 348, pp. 209–212) distinguishes between the states "ventrally weakly inflated" (#109), "strongly inflated" (#110) and "extremely inflated" (#116). According to the list of convergences (fig. 348, caption), the character states given for ampulla shape, "secondarily depressed" (#70), "secondarily depressed, cigar-shaped" (#133) and "depressed" (#146), refer to identical character states. Based on the same source, "spire and visceral hump flattened" (#143), "shell planorboid" (#62) and "shell and visceral hump planorboid" (#127) are also identical. Additional complication is caused by use of the term "reduced" (*reduziert*) instead of presence/absence character states; "reduced" seems to indicate "lost" in some cases, "reduced in size" in others.

It is not always clear how character states were scored. A certain state used in the analysis for a given taxon apparently does not necessarily mean that this state is characteristic for **all** species included. For instance, table 1 (shell characters) gives up to three possible conditions per genus for a character, but only one such condition is selected to construct the "preferred tree." Another example is character state change #145, which marks *Pomacea* (*Ef-fusa*) as having a flattened pericardium, but the text (p. 41) mentions an intermediate condition within that group.

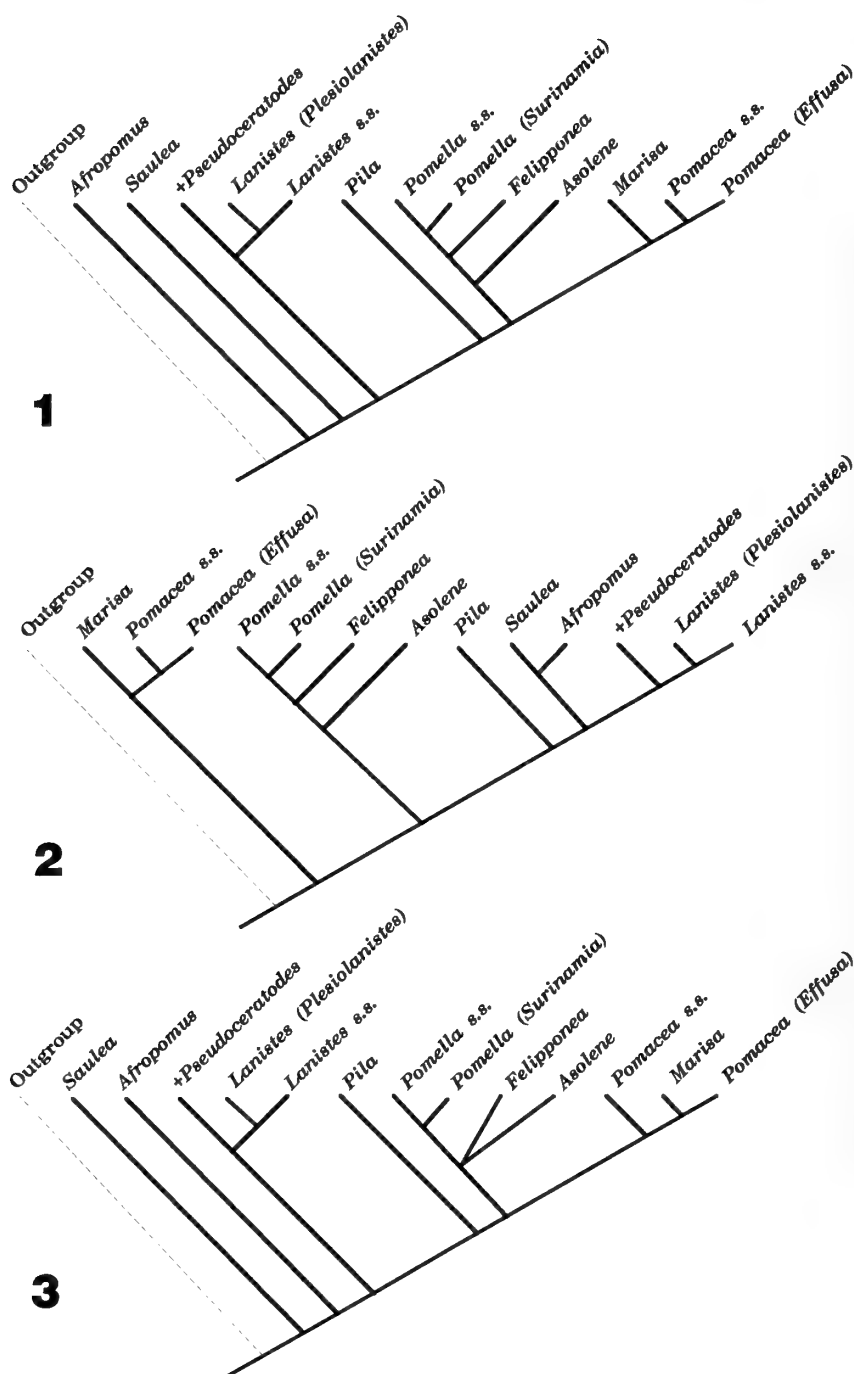
Because no formal data matrix is presented in the work and the various trees are constructed by hand, a rigorous cladistic analysis based on the presented data seems appropriate here. This will provide a formal data matrix as well as an English-language character listing and descrip-

tion. The reanalysis is thus not based on new or different data, but interprets the available information in a reproducible fashion to address the following main questions: Can a resolved most-parsimonious cladogram be constructed from the published character set? If so, how different is it from Berthold's "preferred" version? The most interesting point in this reanalysis certainly lies in whether a "most-parsimonious" cladogram without *a priori* ordering of character states and without weighting differs from one that follows Berthold's "fitness" ordering through adaptational analyses.

I have attempted to reconstruct a formal data matrix (this Figure 4) from the information in text and figures. Because the author did not number characters or character states, but assigned numbers to each character state change, I could not employ his numbering system. In the following, the new numbers assigned for this re-analysis are not preceded by "#" to distinguish them from Berthold's original usage. I included the characters that are synapomorphies at the family level (characters 0–22) to demonstrate the ampullariid characters as defined by Berthold; it is clear, however, that these do not provide any resolution of ingroup relationships. Omitted from the analysis, because uninformative in this context, are binary characters defining only terminal branches (i.e., autapomorphies of the genus-group taxa). The remaining characters were coded as binary or (if unequivocal) as multi-state characters as given below. In case of ambiguous statements within the monograph, information was taken from the descriptions on pp. 209–212 and from the list of convergences in figure caption 348. The outgroup state was inferred as the state opposite to the first change listed in Berthold's cladogram (the author did not employ any particular taxon as outgroup; Viviparidae are mentioned as one possible sister group, and a variety of caenogastropods are used in informal outgroup comparisons). I have made one exception from this procedure; for the fossil genus *Pseudoceratodes*, I have coded all non-shell characters as "unknown." The resulting list comprises 55 binary characters and 15 multi-state characters, totalling 161 character states.

It is important to stress that this is a reconstructed data matrix, because the cells in this matrix show the states Berthold *implied* for individual taxa (by placing character state changes on branches leading to these taxa), and not necessarily always the current state of knowledge for the particular taxon. An example is character state change #101, which infers a proximal penial sheath gland for, among others, *Pomella*. Berthold (p. 184) cites Hylton-Scott (1943; who claimed absence of this structure in *Pomella*), but *assumes* that a penial sheath would be found if the group were studied histologically.

Anatomical features, such as alimentary tract and nervous system, are extensively treated in this work, and it is interesting what characters are deemed informative for a family-wide phylogenetic analysis. Shell features account for 27% (31 states) of the informative characters (i.e., those that influence tree topology), although some of these are



Explanation of Figures 1 to 3

Figure 1. Berthold's preferred hypothesis of phylogenetic relationships within the Ampullariidae, based on his figure 348.

Figure 2. Cladogram derived from data matrix given in Figure 4. All characters sequentially ordered and given equal weight. $l = 244$, $ci = 87$, $ri = 78$; with ingroup symplesiomorphies (characters 0 to 22) omitted: $l = 221$, $ci = 85$, $ri = 78$; one step shorter with characters 30 to 32 coded as 1 instead of 0 for *Plesiolanistes*.

Figure 3. Nelson consensus tree of three equally parsimonious cladograms derived from data matrix given in Figure 4. All characters unordered and given equal weight. $l = 128$, $ci = 85$, $ri = 83$; with ingroup symplesiomorphies (characters 0 to 22) omitted: $l = 105$, $ci = 81$, $ri = 83$; one step shorter with characters 30 to 32 coded as 1 instead of 0 for *Plesiolanistes*. Characters 46, 59, 60, 63 and 65 with retention index < 50 .

	0	1	2	3	4	5	6	7
	0123456789012345678901234567890123456789012345678901234567890							
outgroup	00000000000000000000000000000000-00--0000-00-----000000-000000							
Afropomus	11111111111111111111101000101100110000000000000000000001000000110101							
Saulea	111111111111111111111010001000000110001000001000000100000100000022010							
Pseudoceratodes	1????????????????????11101010????????????????????????????????							
Plesiolanistes	1111111111111111111111111010//00120000111001110110210000000000012011							
Lanistes	111111111111111111111111101001100120000111001110110210000000000012011							
Pila	111111111111111111111010001011000121111001101010131211000000000012111							
Pomella	1111111111111111111111220032311021121111001111021121311101100000012101							
Surinamia	1111111111111111111111220032211021121111001111021121311101100000012101							
Felipponea	1111111111111111111111220022111010121111001111021121311101100000012111							
Asolene	1111111111111111111111220012011000121111001111021121311101100000012011							
Marisa	11111111111111111111111010301100003111011111021121311112101101012011							
Pomacea	1111111111111111111111101000010100013311100111102112131111211112112111							
Effusa	111111111111111111111111100010110000321100111102112131111211112112111							

Figure 4

Data matrix. “?” character state unknown (fossil group), “-” character state not applicable (character not present), “/” character state either 0 or 1.

considered by the author “not a valuable character to reconstruct phylogenetic relationships” (p. 142, my translation). Characters of the female reproductive system, elsewhere in the work described as prone to modifications and convergences (p. 189), account for 20% (20 states). Miscellaneous non-reproductive anatomical characters (25%, 29 states) and male reproductive characters (24%, 28 states) form most of the rest. Data derived from ecology, physiology, and biogeography (as stressed at the onset, p. 8) are hardly realized in the analysis, with only characters 69 and 70, totalling 4 states.

The Analysis

Using the data matrix (Figure 4) the following cladistic analyses were performed, employing the computer program Hennig86 (FARRIS, 1988) on a 486-class personal computer. The "implicit enumeration" algorithm, guaranteeing to find all equally parsimonious trees, was used.

(A) All characters were sequentially ordered according to the sequence implied by Berthold and given equal weight. Two separate runs were made, with characters 30–32 coded for *Plesiolanistes* either as 0 or 1 (the character being variable between populations of the single species included). Subsequent runs deactivated characters 0 to 22 (the in-group plesiomorphies) to attain meaningful numbers on tree length (l), consistency index (ci), and retention index (ri).

(B) The same scenario was repeated, with all characters unordered.

The first (ordered) approach resulted in a single most-parsimonious cladogram (Figure 2). The subclade organization is very similar to Berthold's preferred tree (Figure 1) and includes a presumed monophyletic group *Pomacea* + *Effusa*, but the overall tree topology is almost inverted, with the *Marisa*-*Pomacea*-*Effusa* clade at the bottom. It

appears that Berthold's suggested character state ordering does not support his overall hypothesis of ampullariid phylogenetic relationships.

The second (unordered) approach resulted in three equally parsimonious trees. The consensus tree (Figure 3) is very similar to Berthold's preferred tree (Figure 1). There are only three differences. *Afropomus* and *Saulea* traded places in the lower part of the tree. Two of the three resulting trees resolved *Felipponea* and *Asolene* as in Berthold's tree, while the third placed them as a sister clade to *Pomella* + *Surinamia*. The third difference is that the parsimony analysis placed *Marisa*, not *Pomacea*, as sister taxon to *Effusa*. The relative position of the subclades is obviously very sensitive to ordering of the multistate characters in the data set. The parsimony analysis resulted in a tree topology almost identical to the one proposed by Berthold, without having to resort to character state ordering or character weighting.

Biogeography

In the third section of the monograph, the author offers seven different scenarios to account for the current distribution of ampullariid taxa. Ecological and historical (*i.e.*, tectonic) parameters are discussed in detail. As a result of his biogeographical analyses, Berthold postulates an original Gondwana distribution for the family and states that the oldest ampullariid fossils are from *Pila* in the Eocene of Egypt and Kenya. However, this hypothesis is contradicted by the much older records for *Reesidella* from the uppermost Jurassic and lower Cretaceous of North America and China. This latter group, presumed to be similar to *Pila* in shell and opercular characters (TOZER, 1956; WANG HUI-JI, 1984), remains undiscussed.

In summary, while I disagree with Berthold's methodology of arranging intuitively weighted "evolutionarily

significant" character states into preferred cladograms, it should be noted that such a critical estimate of the author's phylogenetic analysis is only made possible by the extensive documentation of characters in this work. Despite the above points of critique, there is no question that Berthold's monograph contains a wealth of information on the family Ampullariidae. This work, with its detailed anatomical descriptions, will become "required reading" for anyone interested in the family.

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- "autapomorphies." Binary characters defining autapomorphies of terminal taxa omitted.

Unreversed Synapomorphies at Family Level (i.e., only outgroup differs in state)

- (0) shell suture edged: no (0), yes (1 [#2])
- (1) labial tentacles: not present (0), present (1 [#4])
- (2) osphradial length: not shortened (0), shortened (1 [#5])
- (3) lung sac: not present (0), present (1 [#6])
- (4) gill moved to right side: no (0), yes (1 [#8])
- (5) anterior aorta forms ampulla: no (0), yes (1 [#9])
- (6) anterior kidney chamber: not present (0), present (1 [#10])
- (7) bipartite copulatory organ {penis + penis sheath} on right mantle margin: not present (0), present (1 [#11])
- (8) eupyrene and atypical sperm anchored in nurse cells: no (0), yes (1 [#12])
- (9) spermatophore: present (0), reduced (1 [#13])
- (10) pallial oviduct with 3 accessory glands: no (0), yes (1 [#14])
- (11) jaws: not enlarged (0), enlarged (1 [#18])
- (12) number of radular rows: not reduced (0), reduced (1 [#19])
- (13) radular teeth with few but enlarged cusps: no (0), yes (1 [#20])
- (14) inner marginal radular tooth: without basal lobe (0), with basal lobe (1 [#21])
- (15) number of medio-dorsal protractors of buccal mass: not reduced (0), reduced (1 [#22])
- (16) esophageal pouches with demarcated esophageal gland: no (0), yes (1 [#23])
- (17) two median stomach grooves: not present (0), present (1 [#24])
- (18) intestine elongated and repeatedly coiled: no (0), yes (1 [#25])
- (19) pleurosupraintestinal zygois: not present (0), present (1 [#26])
- (20) subintestinal ganglion fused with right pleural ganglion: no (0), yes (1 [#27])
- (21) pleural commissure: not present (0), present (1 [#28])
- (22) pedal and pleural ganglia fused on both sides: no (0), yes (1 [#29])

Characters Informative for Ingroup Relationships

Shell characters (outgroup state = 0)

- (23) shell shape: egg-shaped (0), planorboid (1 [#62, #127, #143]), weakly neritoid (2 [#103])
- (24) whorl shape: moderately bulging (0), strongly bulging (1 [#1]), flattened (2 [#106])
- (25) hyperstrophy: no (0), yes (1 [#61])
- (26) umbilicus: narrow (0), wide (1 [#63, #129])
- (27) spire: not shortened (0), shortened (1 [#104]), further shortened (2 [#107]), extremely shortened (3 [#111])

Appendix

Listing of characters and character states as employed in cladistic reanalysis, derived (translated and interpreted) from Berthold's tree (fig. 348) and listing (pp. 209-212). Numbers in square brackets refer to Berthold's original

- (28) aperture: round (0), broadly oval (1 [#3]), acutely oval (2 [#105]), kidney-shaped (3 [#128])
- (29) aperture: small (0), ventrally weakly inflated (1 [#109]), strongly inflated (2 [#110]), extremely inflated (3 [#116])
- (30) dorsal carina: present (0), reduced (1 [#32, #64, #76, #73-in part])
- (31) median carina: present (0), reduced (1 [#33, #65, #75, #77, #73-in part])
- (32) umbilical carina: not present (0), present (1 [#66, #73-in part])
- (33) longitudinal striping: present (0), reduced (1 [#108]), completely reduced (2 [#112])

Non-reproductive anatomical characters

- (34) visceral hump: not shortened (0), shortened (1 [#34, #114])
- (35) mantle cavity: not broadened (0 [#130, #144; as "narrowed"]), broadened (1 [#7])
- (36) lung sac opening: non-closable (0 [#6]), closable (1 [#37]), with closing tube (2 [#53]), with prolonged closing tube (3 [#121])
- (37) ingestion siphon: not elongated (0), elongated (1 [#78]), further elongated (2 [#137]), extremely elongated (3 [#142])
- (38) ingestion siphon forming breathing tube: no (0), yes (1 [#79])
- (39) lung sac pump breathing: no (0), yes (1 [#80])
- (40) ampulla shape: depressed (0 [#9, #70, #133, #146]), enlarged, vertically egg-shaped (1 [#39])
- (41) auricle-ventricle axis: perpendicular to aorta axis (0), tilted toward aorta axis (1 [#132])
- (42) pericardium: round (0), flattened (1 [#68, #131, #145])
- (43) posterior kidney chamber with lobe: no (0), yes (1 [#55])
- (44) central radular tooth: trapezoidal (0), rectangular (1 [#86])
- (45) pleuro-supraintestinal zygois: not broadened (0 [#26]), broadened (1 [#102])
- (46) cerebral commissure in cross-section: round (0), flattened (1 [#43])
- (47) origin of anterior osphradial nerve moved anteriorly: no (0), yes (1 [#72])

Reproductive characters, male

(outgroup state: not applicable¹)

- (48) penis length: not prolonged (0 [#11]), prolonged (1 [#57]), prolonged and coiled in pouch (2 [#98])

- (49) penial sperm groove: open (0), closed to form central channel (1 [#99])
- (50) penial sheath length: not prolonged (0 [#11]), prolonged (1 [#56])
- (51) distal penial sheath gland: not present (0); epithelial cells at distal inner margin of penial sheath prolonged (1 [#59]); present, weak (2 [#82; *i.e.*, further elongation of cells, see p. 180]), epithelial cells extremely prolonged (3 [#91])
- (52) outer penial sheath gland: not present (0), present (1 [#83])
- (53) penial bulb: not present (0); present (1 [#40]), enlarged (2 [#58]), widened into penial pouch (3 [#97])
- (54) epithelium at base of copulatory organ in grooves: no (0), yes (1 [#60])
- (55) copulatory organ with sperm groove lobe: no (0), yes (1 [#81])
- (56) distal penial sheath gland enlarged by subepithelial glands: no (0), yes (1 [#100])
- (57) distal penial sheath gland with basal lobe: no (0), yes (1 [#123])
- (58) proximal penial sheath gland: not present (0); present, weak (1 [#101]); enlarged (2 [#122])

Reproductive characters, female

- (59) receptaculum seminis with separate exit duct: yes (0 [#71, #93]), no (1 [#16])
- (60) receptaculum seminis moved proximally toward coiled oviduct: no (0), yes (1 [#140])
- (61) pallial oviduct with numerous lateral pouches: no (0), yes (1 [#126])
- (62) shell gland with diverticle: no (0), yes (1 [#124])
- (63) shell gland coiled into primary and secondary helices: no (0), yes (1 [#138])
- (64) pseudo-bursa formed by atrium of receptaculum seminis: no (0), yes (1 [#125]); yes, separated from receptaculum by tube-shaped section of pallial oviduct (2 [#141])
- (65) size of proximal albumen gland: not reduced (0 [#14]); reduced (1 [#139; *i.e.*, small parts present, see p. 184])
- (66) pallial oviduct with albumen gland diverticles: no (0), yes (1 [#15]), reduced (2 [#49])
- (67) bursa copulatrix: normal (0), enlarged (1 [#36]), reduced (2 [#41])
- (68) calcareous egg shell (= egg deposition outside water): no (0 [#120, #134]), yes (1 [#84, #85])

Other characters

- (69) diet: microphagous (0 [#113]), macrophagous (1 [#17])
- (70) sinking behavior with extended foot: no (0), yes (1 [#54])

¹ These characters are not present in the outgroup, and thus no outgroup comparison is possible to infer character polarity in this character suite. The bipartite copulatory organ (penis and penial sheath), as a derivative of the right mantle margin, is an autapomorphy of the Ampullariidae (*e.g.*, the copulatory organ in the presumed sistergroup Viviparidae is a modified right cephalic tentacle).

Questionable Species in the Cephalopod Genus *Argonauta*

by

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HOCHBERG *et al.* (1992) list six species of living *Argonauta* in their discussion concerning larval forms of this genus: *A. argo* (Linnaeus, 1758), *A. nodosa* (Lightfoot, 1786), *A. hians* (Lightfoot, 1786), *A. nouryi* (Lorois, 1852), *A. boettgeri* (Maltzan, 1881), and *A. cornuta* (Conrad, 1854). Of these six species, *A. boettgeri* and *A. cornuta* should be considered questionable.

The shell of *Argonauta boettgeri* (Figure 1A–C), which is very rare, is similar in appearance to that of *A. hians* (Figure 1D–F). On the basis of female arm length (NESIS, 1987), no distinction is made between *A. boettgeri* and *A. hians*, and ROBSON (1932) considers the possibility that *A. boettgeri* is a form of *A. hians*.

Argonauta cornuta has the same eastern Pacific range as *A. nouryi* and the differences between the shells of *A. cornuta* and *A. nouryi* reflect the variation pattern seen in *A. hians* (Figure 1G–K). What distinguishes the shell of *A. cornuta* from that of *A. nouryi* is the presence of what have

been termed “flutes” or “horns” on the shell aperture. The shell of *A. hians* may or may not have flutes or horns on the aperture. To a much lesser degree, flute or horn structures may be present on the shells of *A. argo* and *A. nodosa*.

Until further quantitative work is done on the shell and soft parts of *Argonauta boettgeri* and *A. cornuta*, these species remain questionable. Specimens of *A. boettgeri*, *A. cornuta*, and *A. nouryi* are included in the collection of the California Academy of Sciences, although these specimens have not yet been assigned identification numbers.

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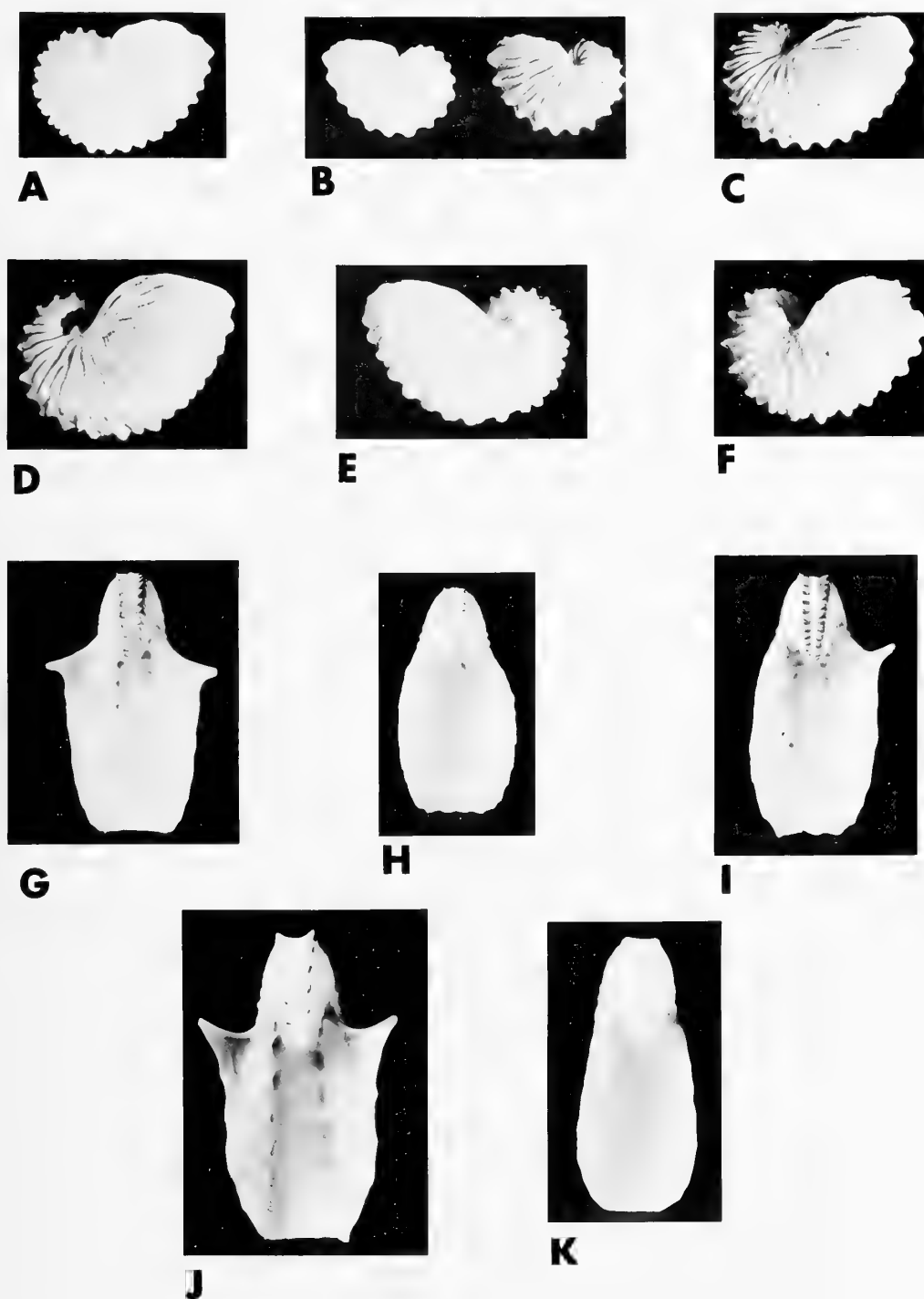


Figure 1

A. *Argonauta boettgeri* (45 mm). B. *A. boettgeri* (32 mm) at left and *A. boettgeri* (33 mm) at right. C. *A. boettgeri* (47 mm). D-F. *A. hians* (54 mm, 47 mm, 52 mm). G. *A. cornuta* (71 mm) aperture view. H. *A. nouryi* (66 mm) aperture view. I. *A. nouryi* (76 mm) aperture view showing characteristics of both *A. nouryi* and *A. cornuta*. J, K. *A. hians* (92 mm, 86 mm) variations, aperture view.

BOOKS, PERIODICALS & PAMPHLETS

Pacific Coast Nudibranchs, Second Edition

by DAVID W. BEHRENS. 1991. Sea Challengers, 4 Somerset Rise, Monterey, CA 93940. vi + 107 pp. Price: \$25.95 (U.S.).

On a recent expedition to the Gulf of California, I had collected an anomalous specimen of *Acanthodoris* which I could not immediately identify. After returning to town, I photographed the animal under the dimming light of a January late-afternoon cloud cover. All that day, the electric generator for the whole town of Bahía de los Angeles had not been working because their diesel supply had run out. Sitting in my hotel room after sunset, by the quivering yellow light of an oil lantern, I determined the species of my unidentified animal using David W. Behrens' second edition of *Pacific Coast Nudibranchs*. This book works under Baja California field-tested conditions! It is scientifically accurate, clearly understandable, and communicates a wealth of information. The descriptions are clear, informative, and relate to living creatures one will find in eastern Pacific intertidal and subtidal regions from Alaska to the tip of Baja California.

Pacific Coast Nudibranchs is a field guide with three main sections: introductory material, species descriptions (the heart of the book), and a classification scheme and literature cited.

The first section is 28 pages of well-written and useful text summarizing what we know about the biology and anatomy of the Opisthobranchia. It describes their general characteristics and evolutionary adaptations (emphasizing their shift from using a protective shell to chemical defensive means). Behrens then presents terse, clear summaries of feeding and the radula, sensory organs and the rhinophores, respiratory appendages, and opisthobranch reproduction. Each topic is superbly illustrated.

The introductory section concludes with a pictorial glossary and dichotomous key to the opisthobranch orders and suborders. The line drawings and key will lead anyone (even someone unfamiliar with the curious anatomical structures of sea slugs) to the correct section of the color photographs of species to identify his or her "slug at hand."

The species descriptions (pages 28-100) include full color photographs of 217 species of opisthobranchs with descriptive notes. For every species, there is a verbal description of the salient external diagnostic features, a radular formula, size, range, and natural history notes. Numerous references document the sources of the information. I found relatively few errors in the text (Elliot, on pages 80 and 102, being the most obvious, misspelling a famous author's name).

Of special note, the author and year citation is given for each species. Some species have their common English

names listed in small print, but many do not; the emphasis is properly on the correct scientific name of the species.

Most of the photographs are excellent, depicting the colors and shapes of these foudroyantly beautiful ocean dwellers. Even casually paging through the book, one frequently pauses on a photograph because of the brilliance of its color, the sharpness of the image, or the marvelous morphological diversity of the organism. Many are obviously aquarium-staged photographs; the best are *in situ* photographs that reveal the biology of the species (e.g., *Phyllaplysia taylori* Dall, 1900, on the seagrass *Zostera*, and *Elysia hedgpethi* Marcus, 1961, on the finger alga *Codium*). Photographing these incredibly colorful organisms, often only 5-25 mm in length, is extremely difficult. Dave Behrens is to be complimented on assembling richly useful photos of all the species he discusses. The combination of introductory keys, descriptions of salient anatomical features, and the excellent photographs almost guarantees the user's ability to identify any Pacific coast opisthobranch.

Concluding the guidebook are a classification scheme of the opisthobranch mollusks described in the book, and three pages of literature cited. The majority of the references were published since 1980 (after the publication of the first edition). This extremely valuable section allows nearly an immediate entrance into the incredibly large number of opisthobranch publications that have appeared in the last decade.

An index to scientific names (thankfully omitting an index to English common names) is on the inside cover and endpage. I think that the addition of another folio of pages (or even half-folio) would have given the author extra pages to spread out a few tight layouts, add some historical information, and include several maps.

One must contrast this new edition with Dave's first edition. The layout of the species descriptions is different; the photograph and description are on the same page, with illustrations therefore appearing on the outer half of each page, rather than text on one page and illustrations on the facing page. This welcome change makes the book far more useful, because one can cursorily thumb through the book to find an animal, without having to open and search the "innards" of every page. Species coverage, quality of photographs, and bibliography are bigger and better than the first edition.

Comparing the two editions, published 10 years apart, documents the progress that has been made in our knowledge and understanding of alpha-level (and higher) taxonomy, evolutionary ecology, and the zoogeography of the opisthobranch gastropods in the eastern north Pacific temperate and cold water faunal regions. The first edition of Dave's *Pacific Coast Nudibranchs* played an instrumental role in stimulating and encouraging a significant amount

of this new research. I believe his second edition will be equally pivotal.

Hans Bertsch

Pacific Coast Nudibranchs: Supplement I. Radula

by DAVID W. BEHRENS. 1992. Sea Challengers, 4 Somerset Rise, Monterey, CA 93940. 11 pp., 150 illus. Price: \$6.95 (shipping and handling \$1.80).

This booklet is a necessary supplement to Dave Behrens' *Pacific Coast Nudibranchs, second edition* (1991). In it are assembled line drawings of the radular teeth of 150 opisthobranch species that occur on the American Pacific coast from Alaska to Baja California. The cover is a beautiful scanning electron micrograph of the radula of the hydroid-feeding eolid nudibranch *Bajaeolis bertschi*.

The introduction is a tersely written summary of the taxonomic uses of radulae (citing my paper on ontogenetic and intraspecific variation of opisthobranch radulae), their overall structure and function, and how to extract and mount a radula for study (referring to Tom Thompson's method), and it includes references for the major sources of the included drawings (MacFarland and McDonald).

When I received this booklet, I spent a lot of time perusing the drawings, thinking about the different shapes, the species' prey items, and reasons for differences and similarities. For instance, the sponge-feeding notaspidean *Anidolyta spongothoras* has radular teeth similar to those of the sponge-feeding nudibranch species of *Cadlina* and other chromodorids, yet is distinctly different from the sponge-feeding teeth of species of *Aldisa*.

This publication highlights the diversity of opisthobranch feeding structures and should encourage much thought and study about their functional morphology. It is highly recommended.

Hans Bertsch

The Genus *Chicoreus* and Related Genera (Gastropoda: Muricidae) in the Indo-West Pacific

by ROLAND HOUART. 1992. Memoires du Museum National d'Histoire Naturelle, Zoologie, tome (A) 154. 188 pp., 480 figures, 4 tables. Price: Dfl 125.00 (about US\$ 74.00) plus postage.

Species of the muricid genus *Chicoreus* Montfort are arguably the most beautiful of the family. Certainly they are the most numerous in numbers of species (about 90 world-wide). And, as they frequently occur in shallow

water or even intertidal environments, they are well-represented in most collections. They are also the most complex of the groups in the Muricinae, as a result of a more than usual amount of intraspecific variation.

Because of the ready availability of specimens, from the time of Linnaeus numerous species have been erected—most without much more than an oftentimes poor illustration in an iconography (e.g., Martini and Chemnitz) to serve as a type, or an even worse original illustration in the case of Perry. With the advent of workers such as Sowerby and Reeve, and Kiener for the species of Lamarck, the illustrations improved considerably and in many cases, though by no means all, there is actually a specimen somewhere upon which the illustration was based. If this model can be located then it is an invaluable type specimen.

Just to give an idea of the magnitude of the problem, Houart has accepted a total of 64 Recent taxa in the three genera he is monographing (*Chicoreus*, *Chicomurex*, and *Naquetia*) but these 64 species have a total of 77 synonyms between them. If one excludes the 16, mostly deep-water forms that have been named since 1980, the numbers are even more daunting: 48 species with 77 synonyms. One well-known species, *Chicoreus brunneus* (Link), alone has 10 synonyms.

To clean up this clutter of taxa is a job second only to the Aegean stables—but Houart has attacked it with the vigor of Hercules and even though I am not 100% satisfied, certainly I can accept the results. It is my personal feeling that it is better for me to decide that this is the final word and let the malacological community re-label their collections one last time than to persist in any disagreement over subjective synonyms.

To establish these synonymies Houart has done an amazing job of locating type material and especially of figuring these obscure types. Of the over 400 illustrations of specimens, one-third represent type material. This alone makes the book worth its somewhat hefty price. But even more than that, the illustrations are uniformly well done, and the four plates of color illustrations are especially gorgeous.

In the systematics there will not be too many changes to cause pain to the collector. Only one "familiar" species has disappeared, that being *Chicoreus penchinati* (Crosse), which has disappeared into the synonymy of *C. strigatus* (Reeve). Species of what heretofore have been considered to be *Chicoreus* s.s. are divided into a subgenus *Chicoreus* s.s., characterized by the presence of a labral tooth, and a subgenus *Triplex* Perry, lacking this tooth. Having participated in the dismemberment of *Murex* s.s. on the same grounds, I can scarcely find fault with this division. One new subgeneric taxon is proposed, *Chicopinnatus* (type species: *Pterynotus orchidiflorus* Shikama), for those few species that have the superficial appearance of the genus *Pterynotus*, with three winged varices, but have the early development of *Chicoreus*.

The two taxa *Naquetia* Jousseaume and *Chicomurex* Arakawa, formerly considered to be subgenera of *Chico-*

reus, are elevated to generic level (these are the "related genera" of the title) on the basis of their radular morphology. I wonder if a better arrangement would not be to have the genus *Naquetia*, with subgenera *Naquetia s.s.* and *Chicomurex*?

In addition to the large number of illustrations of specimens there are also distribution maps for each taxon, and of extreme value are the enlarged drawings of protoconchs for 55 Recent species (often more than one example) and six fossil species.

The general format of the book and its overall excellent quality is a tribute to Philippe Bouchet, of the Museum National d'Histoire Naturelle. From an editorial or production perspective it is hard to find fault, but I would have liked to see the figure numbers for multiple specimens of the same species a little more conspicuous (I have simply underlined them in my copy).

The only serious error that I have encountered is the omission of any explanation for figure 302, which is a specimen of *Chicoreus rubescens* (Broderip, 1833) identified in a subsequent work (Apex, 1992, Vol. 7, Nos. 3-4, fig. 4) as a specimen in Houart's collection—47.8 mm from ?Tahiti.

The only other, less serious, error is the plate explanation for figure 339, which is stated to be a neotype (BMNH 1984076) for *Chicoreus banksii* (Sowerby), but in the text it is correctly stated to be the lectotype of *Murex crocatus* Reeve. The latter name Houart places in the synonymy of *C. banksii*, but here is the one synonymy with which I must take issue. Houart has rightly demonstrated that *C. bourguinati* (Poirier) is one name for the East African (Durban to [?] Sri Lanka) species that most workers have called *C. banksii*. He is of the opinion that the Indo-West Pacific (Malaysia to new Caledonia) form variously

referred to *C. banksii*, *C. crocatus*, and (totally erroneously) *C. axicornis* (Lamarck) is not the same as the East African one.

Although I am completely willing to accept this division, the question becomes what name is to be used for which species. He has selected a specimen in the British Museum to serve as lectotype of *Chicoreus banksii* (BMNH 197478), which is said to have come from "the Moluccas."

This, I believe, is the root of Houart's mistake. First, this large (77.5 mm) shell is not Sowerby's illustrated specimen, which according to the original description (1841, Proceedings of the Zoological Society of London, Pt. 8, p. 140) measures "2.8 poll." [=70.8 mm]. Second, another specimen in the British Museum measures 70 mm in height, is very like the illustration given by Sowerby (1841, Conchological Illustrations, fig. 82), and can be matched to specimens from Zanzibar (e.g., that figured by Vokes, 1978, Annals Natal Museum, Vol. 23, pl. 3, fig. 3).

This latter specimen should have been selected as the lectotype of *Chicoreus banksii*; however, it is not too critical because the larger shell is clearly also an East African specimen. If one compares this "lectotype" of *C. banksii* (Houart's fig. 178) and the lectotype of *C. bourguinati* (Houart's fig. 261) it is obvious that they are conspecific; I can match it also with specimens in my own collection from the Seychelles. I assume that the "Moluccas" locality is just another example of incorrect data in old collections and does not place the species in the western Pacific.

Therefore, it seems to me that the name *Chicoreus banksii* must be returned to the East African population, with *C. bourguinati* as a synonym. For the Indo-West Pacific population the name *C. crocatus* is available.

Emily H. Vokes

In Memoriam

Ralph I. Smith

For years of steadfast service
and contributions to C.M.S.
and invertebrate zoology.

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

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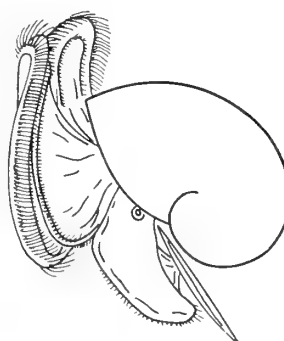
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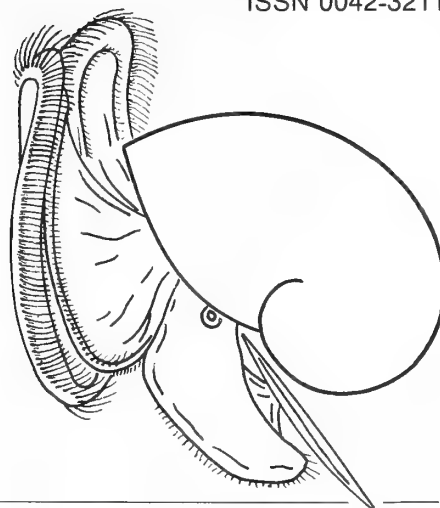
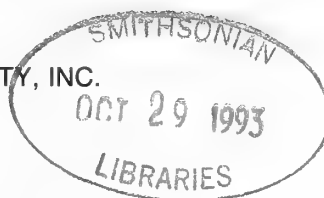
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THE VELIGER

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Local and Regional Abundance Patterns of the Ascoglossan (= Sacoglossan) Opisthobranch *Alderia modesta* (Lovén, 1844) in the Northeastern Pacific

by

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Department of Biology, Syracuse University, Syracuse, New York 13244, USA

Abstract. The ascoglossan (= sacoglossan) opisthobranch *Alderia modesta* (Lovén, 1844) associates with the high intertidal, mat-forming, yellow-green alga *Vaucheria* (Chrysophyta: Xanthophyceae) in temperate estuaries throughout much of the Northern Hemisphere. Although *A. modesta* has been extensively studied on N.E. and N.W. Atlantic shores, complementary information for N.E. Pacific estuaries is sparse. The opisthobranch was common on *Vaucheria* mats in Yaquina Bay and Coos Bay, Oregon, USA with mean densities ranging from tens to hundreds per square meter of algal mat. In Oregon, *A. modesta* was present throughout the entire year. During winter, the ascoglossan persisted on *Vaucheria* within gaps of salt marsh vegetation and in sunny microhabitats with a southern exposure. The opisthobranch numerically dominated the epifaunal invertebrate assemblage associated with *Vaucheria* mats. In northern California, USA, *A. modesta* was sparse in Humboldt Bay and apparently absent from Arcata Bay and Eel River Slough. The species was patchily distributed within Bodega, Tomales, and Drakes bays in California with mean densities <20/m². High densities of predators, particularly shorebirds and the mud-flat crab *Hemigrapsus oregonensis*, may reduce ascoglossan densities in California though other factors may contribute as well.

INTRODUCTION

Estuaries are complex ecosystems composed of several biologically important intertidal habitats including salt marshes, mud flats, and eelgrass beds. One habitat often overlooked is high intertidal algal mats: the yellow-green alga *Vaucheria* (Chrysophyta: Xanthophyceae) forms extensive mats within the lower marsh, in tidal creeks, and on mud flats, downshore from salt marshes. Although *Vaucheria* inhabits and often dominates this habitat in many temperate and boreal estuaries in the Northern Hemisphere (NIENHUIS & SIMONS, 1971; SIMONS, 1974a, b, 1975a, b; JONGE, 1976; POLDERMAN & POLDERMAN-HALL, 1980; GARBARY & FITCH, 1984), basic ecological information on *Vaucheria* and its associated invertebrate fauna is meager (but see HARTOG & SWENNEN, 1952; HARTOG, 1959).

The alga is the primary, or even sole, food of three species of ascoglossan (= sacoglossan) opisthobranchs. In temperate and boreal estuaries throughout the Northern Hemisphere, *Alderia modesta* (Lovén, 1844) associates with *Vaucheria* mats (HARTOG, 1959; BLEAKNEY & BAILEY, 1967; THOMPSON, 1976; BLEAKNEY & MEYER, 1979; MILLEN, 1980; ROGINSKAJA, 1984; BLEAKNEY, 1988). In the N.E. Atlantic Ocean, White Sea, and Barents Sea, the ascoglossan *Limapontia depressa* Alder & Hancock, 1862, coexists with *A. modesta* (THOMPSON, 1976; ROGINSKAJA, 1984). Finally, *Elysia chlorotica* Gould, 1870, is an estuarine species endemic to the N.W. Atlantic that associates with *Vaucheria* and the filamentous green alga *Cladophora* (BAILEY & BLEAKNEY, 1967; CLARK, 1975; BLEAKNEY & MEYER, 1979; BROMLEY & BLEAKNEY, 1979; GRAVES *et al.*, 1979).

Although the ascoglossans have been examined in many

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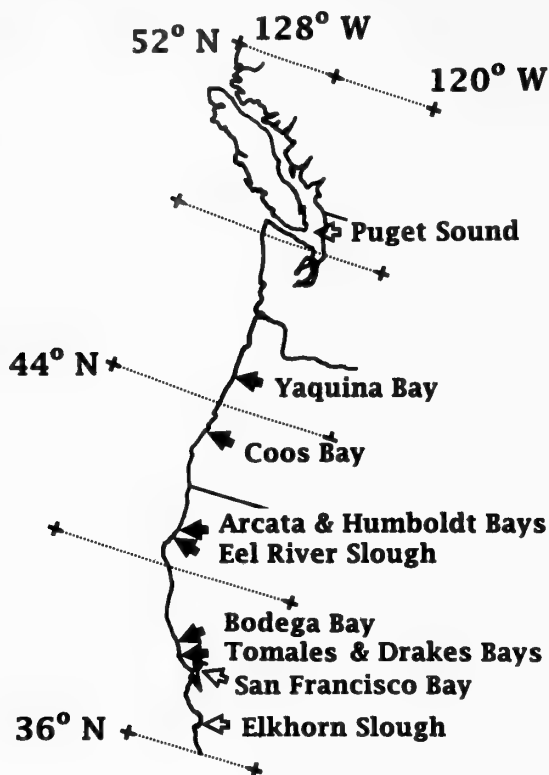


Figure 1

Location of N.E. Pacific estuaries surveyed in this study (solid arrows) and several previous studies (hollow arrows; HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963). Latitudes and longitudes are indicated.

areas of their geographic ranges, information on *Alderia modesta* in the N.E. Pacific is limited (HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963; MILLEN, 1980; TROWBRIDGE, 1993). The species occurs from Vancouver Island, British Columbia (MILLEN, 1980) to Elkhorn Slough, California (STEINBERG, 1963). Within this regional range, *A. modesta* is reportedly common in at least three localities (hollow arrows, Figure 1): Bay Farm Islands in San Francisco Bay and Elkhorn Slough, California, and San Juan Island in Puget Sound, Washington (HAND, 1955; HAND & STEINBERG, 1955; STEINBERG, 1963). Yet, quantitative density estimates are lacking, and the ascoglossan is not included in most other opisthobranch surveys that encompass northern California or Oregon shores. Therefore, this study addresses whether *A. modesta* is widely distributed and abundant in N.E. Pacific estuaries.

NATURAL HISTORY

Alderia modesta has planktotrophic larvae and benthic adults. Larvae settle, metamorphose, and recruit to the algal hosts during spring, summer, and fall in Atlantic

localities (HARTOG, 1959; VADER, 1981), and large adults overwinter in marsh ponds (BLEAKNEY & BAILEY, 1967; BLEAKNEY & MEYER, 1979; BROMLEY & BLEAKNEY, 1979). The ascoglossan grows to sexual maturity about 10 days after metamorphosis (SEELEMAN, 1967). Maximum slug size ranges from 5 to 16 mm, depending on locality (ENGEL *et al.*, 1940; HARTOG, 1959; BLEAKNEY & BAILEY, 1967). In the N.E. Pacific, the reported maximum size of *A. modesta* ranges from 6 to 8 mm (HAND & STEINBERG, 1955; BLEAKNEY, 1988; TROWBRIDGE, 1993). The species apparently manifests no endemism or local morphological variation despite its wide geographic distribution (BLEAKNEY, 1988).

Although HARTOG (1959) noted that *Alderia modesta* associated with some, but not all, estuarine species of *Vaucheria*, little is known about specific algal-host associations. At least four species of *Vaucheria* occur in the N.E. Pacific (GARBAR & FITCH, 1984; SCAGEL *et al.*, 1986): *V. intermedia* and *V. thuretii* are summer to fall species whereas *V. litorea* and *V. longicaulis* are fall to spring species (CONOVER, 1958; NIENHUIS & SIMONS, 1971; SIMONS, 1975a; POLDERMAN & POLDERMAN-HALL, 1980). Because the coenocytic algal filaments interweave (JONGE, 1976), species identification is difficult. Thus, in this study, I did not identify the species composing the *Vaucheria* mats examined.

METHODS AND MATERIALS

Local Patterns

Because the alga *Vaucheria* and ascoglossan *Alderia modesta* are not widely recognized as common estuarine species in the N.E. Pacific and because the herbivore occurs almost exclusively on or around *Vaucheria* mats, I collected information on the distribution of the alga in Yaquina and Coos bays on the central coast of Oregon, USA (Figure 1). During the summers of 1990 and 1991, I walked the shoreline for several hundred meters at every access point on the bays, searching for the alga.

I selected two well-developed regions of algal mats in Yaquina Bay for monitoring of *Alderia modesta*. At each of the two sites, I marked 50-m transects directly downshore from the salt marsh. From May 1990 to January 1992, I surveyed these regions at periodic intervals. During each survey, I examined 10 to 52 randomly selected 0.25-m² quadrats along each transect line. I counted the number of epifaunal *A. modesta* within each quadrat. Because the density of epifaunal ascoglossans declined with increased exposure time, I started counting immediately upon aerial exposure on ebbing tides. To determine whether *A. modesta* was the major invertebrate associated with the algal mats, I also quantified all other taxa encountered in the quadrats. Furthermore, in November 1990, I measured the percent cover of the *Vaucheria* beds, width of beds downshore from the salt marsh, and height of beds above the adjacent mud flat.

Regional Patterns

To evaluate whether the algal-ascoglossan patterns observed in Oregon were typical of other estuaries in the N.E. Pacific, I surveyed Arcata and Humboldt bays and Eel River Slough in Humboldt County, California (Figure 1) in May 1992. Furthermore, I visited Bodega Bay in Sonoma County and Tomales and Drakes bays in Marin County, California (Figure 1) in July 1990 and May 1992. I looked for *Vaucheria* and *Alderia modesta* at most of the public access points around each bay (based on CALIFORNIA COASTAL COMMISSION, 1991).

In areas that I found the alga, I quantified ascoglossan density in 8 to 15 haphazardly selected quadrats (each 625 cm²) of the lushest, greenest sections of the algal mat, where ascoglossans were typically abundant. These values provided estimates of peak ascoglossan densities. Next, I stretched a 15-m transect line along the *Vaucheria* zone and examined 10 to 15 randomly selected 0.25-m² quadrats along each transect. I counted the ascoglossans in each quadrat and calculated mean population densities. To facilitate comparisons of values from different studies using a variety of quadrat sizes (1 dm² to 1 m²), I present all densities of *Alderia modesta* as numbers per square meter. In May 1992, I also measured the maximum size of *A. modesta* at each site to determine the extent to which ascoglossan size varied regionally.

Between-site variation in ascoglossan populations may be due to differences in predator assemblages: shorebirds appeared to consume *Alderia modesta* in Norway (VADER, 1981), and estuarine fishes and shore crabs readily consumed the ascoglossan in Oregon (Trowbridge, unpublished data). Therefore, in July 1990 and May 1992, I noted the presence or absence of shorebirds and shore crabs at each census location.

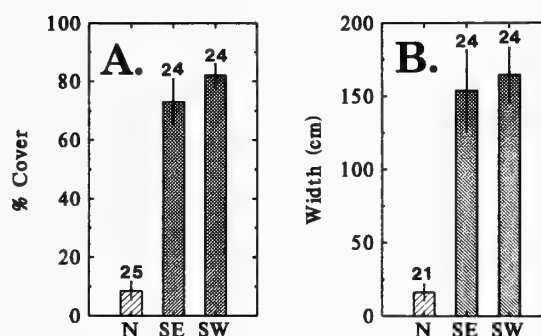
RESULTS

Local Patterns

Algal distribution: In Yaquina Bay, the alga *Vaucheria* occurred in two areas. On the south shore (Figure 2), the alga covered 70–80% of the area along two transects (SE and SW) directly below the salt marsh and formed extensive mats about 150 cm broad and 1.5 to 3 cm tall (above the mud flat). On the north shore (N), the *Vaucheria* bed covered only about 10% of the substrate sampled and was relatively narrow (about 20 cm) and thin (<1 cm) (Figure 2). The alga formed discrete “patch islands” below the marsh.

In Coos Bay (Figure 3), the alga was extremely sparse (1) near the mouth of the bay where the beaches were muddy sand and (2) in many of the sloughs that had pebbly to rocky substrate. Much of Coos Bay was highly channelized due to logging: the alga occurred only in trace amounts within the marsh in these areas. *Vaucheria* was not common where low marsh vegetation (e.g., the pickleweed *Salicornia virginica*) was missing.

Vaucheria Beds



Yaquina Bay, Oregon

Figure 2

Description of the *Vaucheria* beds in Yaquina Bay, Oregon. Data were collected in November 1990. Error bars denote ± 1 SE. Values above each bar indicate the number of replicate 0.25-m² quadrats examined.

In South Slough of Coos Bay (Figure 3), however, *Vaucheria* formed extremely thick, lush mats during the summer. At the mouth of the slough, the alga formed mats fringing the marshes and “patch islands.” The latter were

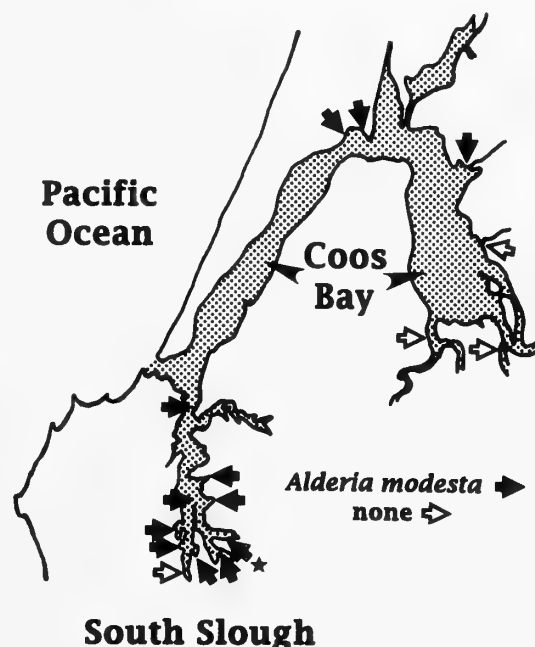


Figure 3

Distribution of *Alderia modesta* in Coos Bay, Oregon, during the summer of 1991. Solid arrows denote areas with *A. modesta*; hollow arrows denote areas without the ascoglossan. The star denotes the site with peak ascoglossan density (about 5000/m² in September 1991).

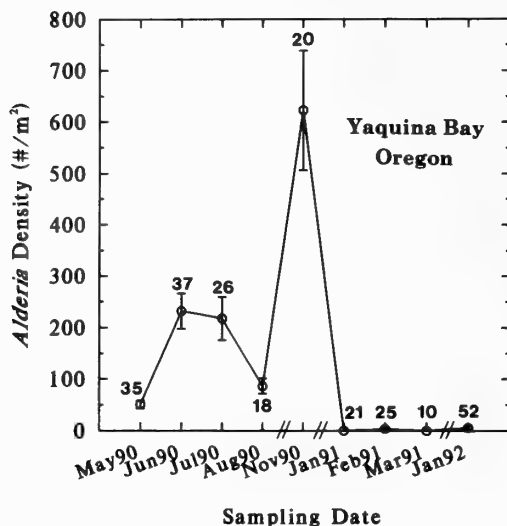


Figure 4

Temporal abundance pattern of *Alderia modesta* on the south side of Yaquina Bay (Idaho Point Road), Oregon. Error bars denote ± 1 SE. Values above each circle indicate the number of replicate 0.25-m² quadrats examined.

stable structures, 15 to 30 m in length, that persisted throughout the year. Although the alga was extremely sparse on the extensive mud flat flanking the main channel of the slough, *Vaucheria* dominated the substrate directly downshore of the marsh vegetation in many of the side tributaries. These regions historically had been diked pastures but subsequently reverted to salt-marsh and mud-flat communities. This historical change is typical of many estuaries in Oregon and northern California.

Ascoglossan abundance: *Alderia modesta* occurred on most of the well-developed *Vaucheria* mats in Yaquina Bay and South Slough of Coos Bay. Mean ascoglossan density ranged from tens to hundreds per square meter of algal mat. Peak densities in individual quadrats were 2152/m² in November 1990 in Yaquina Bay and about 5000/m² in September 1991 in the upper reaches of South Slough (star symbol in Figure 3).

Alderia modesta was present during the entire year (Figure 4) except following an abnormally cold storm in December 1990 when the temperature dropped below freezing for a week, and extensive mortalities of intertidal invertebrates occurred. In February and March 1991, *A. modesta* populations in Yaquina Bay had not yet recovered: no ascoglossans were observed despite extensive searching. In South Slough of Coos Bay, however, low densities of *A. modesta* were found on *Vaucheria* in gaps within the marsh vegetation. For example, based on 19 quadrats examined (each 625 cm²), mean ascoglossan density was 290/m² (SD = 368). No ascoglossans were found on exposed *Vaucheria* mats below the South Slough marsh.

During the following winter, freezing weather did not

occur, and *Alderia modesta* persisted, although the species' distribution was extremely patchy. For example, in January 1992, few ascoglossans persisted on the *Vaucheria* bed below the marsh on the south side of Yaquina Bay (Figure 4) although adults did occur in gaps in the marsh vegetation. On the north side of the bay (with a southern exposure), however, the algal mats were extremely lush, and ascoglossans were abundant: >800/m² based on 10 haphazardly selected 0.25-m² quadrats. Thus, the seasonal persistence of *A. modesta* in Oregon was associated with local variation in microhabitats.

Invertebrate assemblage: *Alderia modesta* numerically dominated the invertebrate assemblage associated with *Vaucheria* mats. Based on nine pooled censuses from May 1990 to January 1992 in Yaquina Bay, the ascoglossan composed 99% of the epifaunal community ($n = 5708$ invertebrates). Insects, particularly larval and adult chironomids, were often present on *Vaucheria* mats, though in extremely low densities.

Regional Patterns

Distribution: In May 1992, I found little *Vaucheria* and no *Alderia modesta* at access points of Arcata Bay or the nearby Eel River Slough. Both drainage basins were primarily high-energy environments with marsh banks severely undercut by erosion. The South Jetty region of Humboldt Bay, however, was a low-energy environment with trace amounts of *Vaucheria* and some *A. modesta* in the muddy sand region. The south bay area within the U.S. Fish & Wildlife refuge appeared, from a distance, to be ideal for the alga and ascoglossan—a muddy, low-energy environment with well-developed marsh vegetation. The area, unfortunately, could not be feasibly sampled due to limited safe access. Most of the areas visited in Sonoma and Marin counties, however, had well-developed *Vaucheria* mats.

Abundance: When I haphazardly selected lush portions of the algal mats, the density of *Alderia modesta* (Figure 5) was moderately high at two sites in California: >100/m² at Bodega Marine Laboratory Research Reserve in Bodega Bay and at Inverness in Tomales Bay. These values represent peak abundances calculated from small spatial scales (625-cm² quadrats). When I counted ascoglossans in randomly selected quadrats (each 0.25 m²), mean *A. modesta* densities ranged from 2 to 20 slugs per square meter (Figure 5). Therefore, even though small patches of *Vaucheria* in California had moderate densities of *A. modesta*, randomly determined densities were quite low: about 1 to 2 orders of magnitude lower than in Oregon.

Ascoglossan size: The maximum length of *Alderia modesta* varied little among sites in California and other areas in the N.E. Pacific (Table 1). Peak ascoglossan size was 9 mm in May 1992 at Doran Beach in Bodega Bay, California. Although size-frequency data were not collected for *A. modesta* in California, few small individuals were

observed. Qualitatively, average ascoglossan size was greater in California than in Oregon.

Potential predators: Small, migrating shorebirds (*e.g.*, plovers, sanderlings) were common at many sites in California in July 1990 and May 1992 but generally not observed in Oregon estuaries (Table 2). Furthermore, the density of shore crabs, particularly the mud-flat crab *Hemigrapsus oregonensis*, was much higher in California than in Oregon. I found up to 10 crabs in every quadrat surveyed in California and no crabs in quadrats in Oregon.

DISCUSSION

Distribution and Abundance

Local patterns: *Alderia modesta* was patchily distributed on a local scale. Part of this variation was associated with the relative abundance of places for the ascoglossans to hide during emergence. HARTOG (1959) noted that slug densities were low when the *Vaucheria* bed was closed (*i.e.*, tightly interwoven algal filaments) because of the difficulty for slugs to burrow and hide. Most *A. modesta* occurred along the margins of cover, around the open spaces in vegetation, and in shrinking rents in the substrate during emergence (HARTOG, 1959; C. D. Trowbridge, personal observations). Furthermore, I observed that the ascoglossans hid in surface depressions of the *Vaucheria* mats, invertebrate burrows (crabs, clams, polychaetes), and in holes produced by feeding shorebirds. It is not known whether *Vaucheria* mats differing in surface texture represent different algal species or a single species under different environmental conditions.

Predation by shorebirds and crabs presumably contrib-

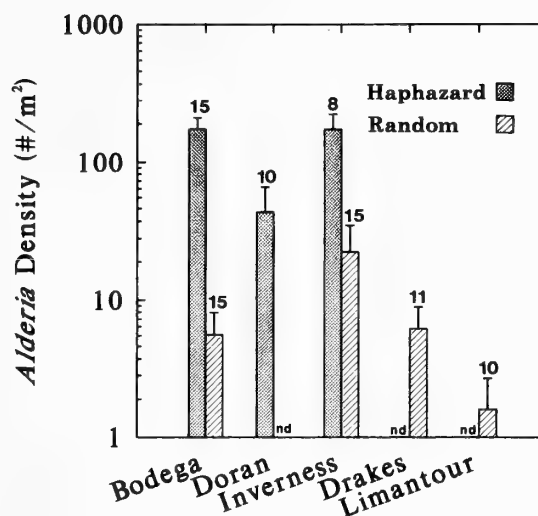


Figure 5

Density of *Alderia modesta* in haphazardly placed and randomly selected quadrats. Bodega Marine Laboratory Research Reserve and Doran Beach are in Bodega Bay; Inverness is in Tomales Bay; Drakes and Limantour esteros are in Drakes Bay, California. The symbol "nd" denotes no data collected. Error bars denote ± 1 SE. Values above each bar indicate the number of replicate quadrats examined.

uted to the patchy distribution of ascoglossans. VADER (1981) reported that Little Stints (*Calidris minuta*) regularly occupied the *Vaucheria* zone in Norway, and he observed that the birds consumed *Alderia modesta* and/or their egg capsules. Furthermore, Trowbridge (unpub-

Table 1

Maximum reported length of *Alderia modesta* in the N.E. Pacific. Sample sizes (*n*) denote number of ascoglossans examined. The symbol "na" indicates that sample size was not provided by authors.

Locations	Body length (mm)		References
	Maximum	<i>n</i>	
British Columbia			
Bamfield Marine Station	6	12	BLEAKNEY, 1988*
Washington			
Friday Harbor Labs	7	10	BLEAKNEY, 1988*
Oregon			
Yaquina Bay	6	148	TROWBRIDGE, 1993
California			
Doran Beach	9	27	this study†
Bodega Marine Lab Reserve	7	184	this study†
Inverness	5	171	this study†
Drakes Estero	4	18	this study†
Limantour Estero	3	4	this study†
Elkhorn Slough	8	na	HAND & STEINBERG, 1955

* Data not collected for specific purpose of determining maximum length of local population.

† Data collected during the May 1992 survey.

Table 2

Visual assessment of the abundance of shorebirds and mud-flat crabs (*Hemigrapsus oregonensis*) on *Vaucheria* in several N.E. Pacific estuaries. Data for Oregon sites were based on several months of observations whereas data for California sites were based on two surveys (July 1990 and May 1992).

Locations	Shorebirds	Mud-flat crabs
Yaquina Bay, Oregon		
Bay Road	absent	absent*
Idaho Point Road	absent	absent*
Coos Bay, Oregon		
Main Branch†	absent	absent
Charleston Bridge	absent	absent*
South Slough†	absent	absent
Bodega Bay, California		
Doran Beach	abundant	abundant
Research Reserve	abundant	abundant
Tomales Bay, California		
Walker Creek	absent	absent
Alan Sieroty Beach	absent	abundant
Millerton Point	absent	abundant
Inverness	abundant	abundant
Drakes Bay, California		
Drakes Estero	absent	abundant
Limantour Estero	absent	very abundant

* Low densities of crab burrows observed at site but not in quadrats.

† Many locations pooled (see Figure 3).

lished data) found that predators (probably fishes and crabs but not birds) significantly reduced populations of *A. modesta* in Yaquina Bay, Oregon. Yet, although predation may reduce ascoglossan densities, the burrowing behavior and small size of *A. modesta* presumably would offer some protection from predators: total exclusion of ascoglossans seems unlikely.

Another potentially important source of variability in slug density was the recruitment rate of larval ascoglossans. Information on patterns of water circulation and larval transport within N.E. Pacific estuaries is limited. Water masses containing larvae may not penetrate all the tributaries of the estuaries (e.g., Walker Creek near the mouth of Tomales Bay), thus explaining the absence of *Alderia modesta*. Alternatively, abiotic factors such as salinity fluctuations may exclude ascoglossans from some locations. ENGEL *et al.* (1940) reported that *A. modesta* can survive at salinities from about 2 to $\geq 37\text{‰}$ though the effects of low salinity on ascoglossan growth and fecundity are not known.

Regional patterns: *Alderia modesta* was often abundant, ranging from tens to thousands of animals per square meter throughout its geographic range. For example, HARTOG (1959) reported 20 to 56 individuals per square meter in

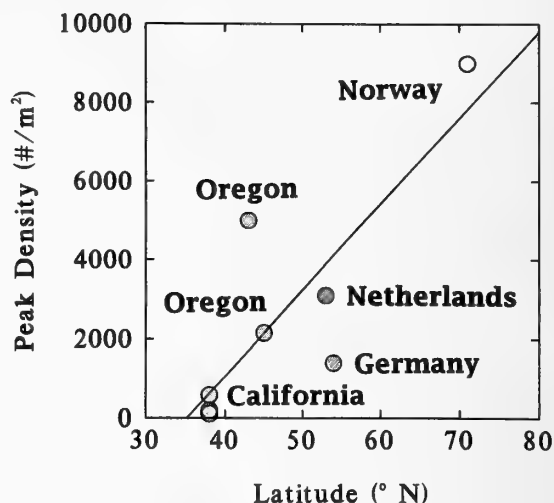


Figure 6

Relationship between peak ascoglossan density and latitude. Data are from this study (Oregon, California) and previous studies (HARTOG, 1959; SEELEMANN, 1967; VADER, 1981).

the Netherlands with a peak density of 3100/m². SEELEMANN (1967) observed 1400/m² on the German Baltic coast. VADER (1981) reported that densities of 500 to 1500 ascoglossans/m² were typical of most sites in Norway; at Klubbukt, however, the mean density was 4820/m² with a peak value of 9000/m². Density values for Oregon and California were, therefore, comparable to values from N.E. Atlantic localities.

CLARK & DE FREESE (1987) reported an increase in multispecies ascoglossan density from low to high latitudes. A similar pattern was seen for a single species (*Alderia modesta*, Figure 6). The correlation was highly significant ($r = 0.825$, $P = 0.012$, $n = 8$ sites) even though the data were from different locations, years, and seasons as well as based on different sample and quadrat sizes. At least three factors may account for the latitudinal trends in population density: (1) decrease in predation intensity, (2) increase in algal productivity (CLARK & DE FREESE, 1987), or (3) increase in larval recruitment with increased latitude. This study provides some evidence supporting (1), but predation was not the sole factor. Although *Vaucheria* beds were generally lusher in Oregon than California, algal productivity probably did not constrain ascoglossan populations in California for two reasons. First, the alga was not a limiting resource for the ascoglossans. Second, maximum body length did not differ much for populations throughout the N.E. Pacific (Table 1). The paucity of juvenile ascoglossans in California and abundance of small individuals in Oregon (TROWBRIDGE, 1993) support the recruitment hypothesis (3). The relative importance of predation intensity, algal quality (as food and substratum), and larval recruitment need to be further elucidated for us to understand regional differences in ascoglossan populations.

Ecological Effects

As the numerically dominant invertebrate associated with *Vaucheria* mats, *Alderia modesta* has two ecological roles within the estuarine food web: (1) as a stenophagous consumer and major herbivore of the algal mats and (2) as prey for estuarine predators. Ascoglossan herbivory may be important to algal hosts under conditions of high feeding rates and/or high population densities (CLARK, 1975; TROWBRIDGE, 1992). Information on feeding rates of *A. modesta* are meager. EVANS (1953) commented on the rapid feeding rate of the ascoglossan: 10 *Vaucheria* filaments per minute. This value, however, is difficult to evaluate because filament size was not given. Because herbivory may be important to algal hosts when ascoglossan density is high, ascoglossan herbivory in Oregon estuaries may contribute to the periodic fragmentation of *Vaucheria* mats.

High densities of *Alderia modesta* in Oregon estuaries suggest that ascoglossans may represent an important food source to estuarine fishes, crabs, and perhaps birds. Although predators rapidly reduced densities of *A. modesta* in August 1990 in Yaquina Bay (Trowbridge, unpublished data), feeding preferences of predators may change ontogenetically or seasonally. For example, small (<10 cm) staghorn sculpins (*Leptocottus armatus*) voraciously consumed *A. modesta* whereas larger conspecific fish (>15 cm) ignored the small opisthobranchs (Trowbridge, unpublished data). Thus, the ascoglossan may be either (1) an important food base within high intertidal, estuarine habitats or (2) a minor prey base sampled by a diverse array of inexperienced juvenile predators. In summary, the ecological role of *A. modesta* merits further attention, particularly at high latitudes where ascoglossan densities are high.

ACKNOWLEDGMENTS

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The Influence of Olfactory and Tactile Stimuli on the Feeding Behavior of *Melibe leonina* (Gould, 1852) (Opisthobranchia: Dendronotacea)

by

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Abstract. The nudibranch *Melibe leonina* feeds using the rhythmic movements of its large oral hood to capture small crustaceans that are present in the water column. The frequency of these feeding movements, or hood closures, is proportional to the concentration of available prey. The purpose of this study was to determine what qualities of prey cause the rate of these feeding movements to change. Animals were observed during exposure to the following treatments: (1) filtered seawater; (2) *Artemia*-conditioned seawater (smell); (3) small particles in seawater; (4) particles soaked in *Artemia*-conditioned seawater; (5) frozen *Artemia* and; (6) live *Artemia*. Both conditioned water and particles caused appetitive behavior (orientation of the oral hood) and a significant increase in the frequency of hood closures. This increase in rate had a rapid onset and was maintained throughout the duration of the 20-min test period. The major difference between the effects of the two stimuli was that smell alone led to incomplete feeding cycles while particle treatments yielded normal feeding behavior. When applied together these stimuli produced a larger response than either one did alone. However, no combination of stimuli was as effective as live prey. We conclude that both tactile and chemical cues are sufficient to elicit an increase in the feeding movements of *Melibe leonina*, but some additional stimulus provided by live prey, such as vibrations, may play an important role as well. The information provided by these stimuli helps initiate appetitive and early aspects of the consummatory phases of feeding, and also influences full expression of the rhythmic feeding motor program.

INTRODUCTION

In most mollusks, both chemical and tactile stimuli have a strong influence on feeding behavior (KOHN, 1983; AUDESIRK & AUDESIRK, 1985). The presence of chemoreceptors in the oral region of many mollusks has been well documented, as has the ability of food extracts to elicit both the appetitive and consummatory phases of feeding

(KOHN, 1961; CROLL, 1983). Mechanoreceptors, which often have centrally located somata, are found both around the mouth and in various regions of the esophagus and gut, and they appear to be capable of either exciting or inhibiting feeding and swallowing behaviors. However, the relative influence of each type of stimulus on feeding behavior has only been examined closely in a few species.

In *Aplysia*, as in many mollusks, there is a clear appetitive response to the presence of chemical stimuli (PRESTON & LEE, 1973; KUPFERMANN, 1974). Animals wave their head, and lift the anterior two-thirds of their body off the

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substrate. If head waving does not bring them in contact with food, they alternate locomotion and head waving until food is localized. Chemical stimuli alone (seaweed extract), when applied to the lips, or mouth region, will elicit a biting response, while tactile stimuli alone (a glass rod) will not (ROSEN *et al.*, 1982). Nevertheless, tactile stimuli will enhance the response to chemical input, resulting in regular biting. *Tritonia diomedea* (Bergh, 1894) also bites repeatedly in response to chemical input (sea whip extract), and as with *Aplysia*, tactile stimuli in the mouth or esophagus modulates this behavior (AUDESIRK & AUDESIRK, 1979). Some interesting mechanoreceptor cells, which also receive excitatory chemical input from the oral veil and mouth region, appear to be at least one site where the two modalities might undergo peripheral integration (AUDESIRK & AUDESIRK, 1980a, b).

The dendronotacean opisthobranch *Melibe leonina* (Gould, 1852) is an unusual gastropod lacking jaws, a radula, and a well-defined buccal mass (GOSLINER, 1987). It feeds by removing small planktonic animals from the water column using a specialized oral hood (AGERSBORG, 1921; HURST, 1968; AJESKA & NYBAKKEN, 1976). This structure is equipped with sensory, muscular, and vascular elements that allow for the efficient capture of free-swimming prey (HURST, 1968). The oral hood surrounds prey that are in the water column, closes to force water out through the tentacles on the edge of the veil, and then contracts further to bring the captured animals into the mouth (WATSON & TRIMARCHI, 1992). If sufficient prey are available, the behavior is rhythmic, with a frequency ranging from 0.5 to 3 cycles/min, depending on the concentration of food in the water (WATSON & TRIMARCHI, 1992).

At the present time little is known about the motor programs underlying expression of rhythmic feeding in *Melibe*, or the sensory inputs that control and influence their expression. The fact that the feeding rhythm is stereotyped (WATSON & TRIMARCHI, 1992), and occurs with a slow rhythm in the absence of prey (AJESKA & NYBAKKEN, 1976; THOMPSON & CRAMPTON, 1984) suggests that a central pattern generator may be involved. *Melibe* is sensitive to tactile stimulation (BICKELL & KEMPF, 1983) and there is some evidence that the feeding cycles are triggered by contact of prey with the oral hood (HURST, 1968). However, no information is available about the possible role of chemoreceptors. The hypothesis put forth by WATSON & TRIMARCHI (1992) is that the feeding rhythm is under the control of a central pattern generator (CPG), and both chemical and tactile stimuli modulate this CPG. The goal of this study was to determine the relative influence of chemical and mechanical stimuli on *Melibe* feeding behavior.

MATERIALS AND METHODS

All animals were collected, using SCUBA, from an eelgrass bed located along the border of the San Juan Channel, near an area of Shaw Island called Neck Point. Shaw

Island is part of an archipelago of 172 islands in the upper Puget Sound, Washington, known collectively as the San Juan Islands. Animals were shipped to New Hampshire and maintained in recirculating aquaria at 10–15°C, in the Zoology Department, U.N.H., Durham, New Hampshire. Animals were starved at least 7 days prior to testing. Feeding experiments were performed in a 15-L aquarium, at 12°C. Three to four animals were placed in the aquarium and allowed to acclimate for 30 min. The feeding activity of each animal (number of hood closures/min) was monitored for 20 min before and throughout each 20-min treatment. In addition, we determined whether each feeding act was complete, according to the criteria described by WATSON & TRIMARCHI (1992). This allowed us to calculate the percent of feeding cycles that were prematurely terminated for each treatment.

Animals were exposed to the following substances: (1) filtered seawater (control); (2) water conditioned with *Artemia* (smell); (3) small (350 μ m) Sephadex beads in filtered seawater (particles); (4) Sephadex beads soaked overnight in *Artemia*-conditioned seawater (smell and particles); (5) frozen *Artemia*; and (6) live *Artemia*. Stimuli were added as concentrated 50-mL aliquots so that when they were diluted in the 15-L aquarium, a final concentration of 1500 particles, or *Artemia*/L, or the odor equivalent to 1500 *Artemia*/L, was obtained. Although *Artemia* is not a normal component of the diet of *Melibe* it was used as a food source because it provides a well-defined and quantifiable diet, and our subjects ate them as voraciously as natural prey. Several preliminary studies with natural prey yielded comparable results.

Statistical analyses were performed using the program SYSTAT (SYSTAT Inc., Evanston, IL.). Ten *Melibe* were randomly chosen for each treatment. The effects of each treatment on complete and on incomplete feeding cycles were analyzed using a one-way analysis of variance (ANOVA) model (SOKAL & ROHLF, 1981). In some cases data were $\ln(x + 1)$ transformed to uncouple the variance from the mean and to give a positive value (KREBS, 1989). A Student-Newman-Keuls multiple comparison was used to detect differences between treatments. To compare the control with individual stimuli, *t*-tests were utilized.

In some experiments animals were sequentially exposed to different treatments to more accurately compare the relative responsiveness of individuals to different stimuli. For example, after 20 min exposure to control conditions, animals were subjected to a 20 min period during which only particles were present, followed by 20 min exposure to smell and particles. These treatments were not independent and were not used for statistical analysis. Rather, they provided information about the additive effects of stimuli and the time course of their influences.

RESULTS AND DISCUSSION

In the absence of any stimuli, in control seawater, *Melibe* maintained a hood closure rate of 0.20 cycles/min ($n = 51$, SEM = 0.017). None of the controls for the various

treatments was significantly different from each other (ANOVA $F = 1.854$, $df: 5, 54$ $P = 0.122$). This allowed comparisons between experimental treatments to be made. The addition of *Artemia*-conditioned water (smell) caused a significant, and rapid, increase in rate ($t = 2.79$ $df = 18$, $P = 0.0016$) (Figures 1, 2, 3). This elevation in rate was maintained for approximately 15 min, before beginning to decline. All the *Melibe* tested ($n = 10$) became more active and oriented their oral hood toward the source of the stimulus. The majority (70%) of the animals tested also began to swim shortly after application of the stimulus. However, this swimming activity was transient, lasting 2–7 min.

The addition of a tactile stimulus (Sephadex beads, particles) also caused a significant increase in hood closure rate ($t = 3.318$, $df = 18$, $P = 0.006$) (Figures 1, 2, 3). As observed with the olfactory stimulus, animals oriented with their oral veil facing the source of the particles, and in 30% of the cases they swam for periods of time ranging from 1 to 9 min. In contrast to their response to the olfactory stimulus, a high hood closure rate was maintained throughout the observational period.

There was no significant difference between the effectiveness of odor and particles as feeding stimulants, although the rate obtained in the tactile treatment was slightly higher (Figures 1, 2). Both treatments resulted in increases in hood closure rate that were approximately one-third as great as those obtained when live food was present (Figure 2). In order to try and mimic the stimuli present when real prey is available, we exposed animals to smell and particles together, particles soaked in *Artemia*-conditioned water, or frozen *Artemia*. These treatments did elicit greater responses than either stimulus applied alone, but there was no significant difference between the soaked particle, frozen *Artemia*, or inert particle treatment (Figure 2). Moreover, none of these treatments was nearly as effective as live prey. Thus, both tactile and chemical cues are sufficient to elicit an increase in the rate of feeding movements of *Melibe leonina*, but some additional stimulus provided by live prey, such as vibrations, probably plays an important role as well.

In order to determine if olfactory and tactile stimuli had additive influences on feeding movements we examined the effects of adding them sequentially. Both treatments, by themselves, resulted in a rapid increase in hood closure rate (Figure 3). However, the addition of a second, different stimulus, 20 min after the initial stimulus, did not result in any further increase in the hood closure rate of the animals tested. In contrast, addition of live prey to the observation chamber, produced a significant increase in rate. The findings of this experiment reinforce the hypothesis that live prey provide an additional feeding stimulus which excites *Melibe* feeding activity more than any combination of smell or inert particles.

WATSON & TRIMARCHI (1992) proposed that the feeding motor program of *Melibe* consists of a central pattern generator which is modulated and regulated throughout the feeding cycle by sensory input. They noted that animals

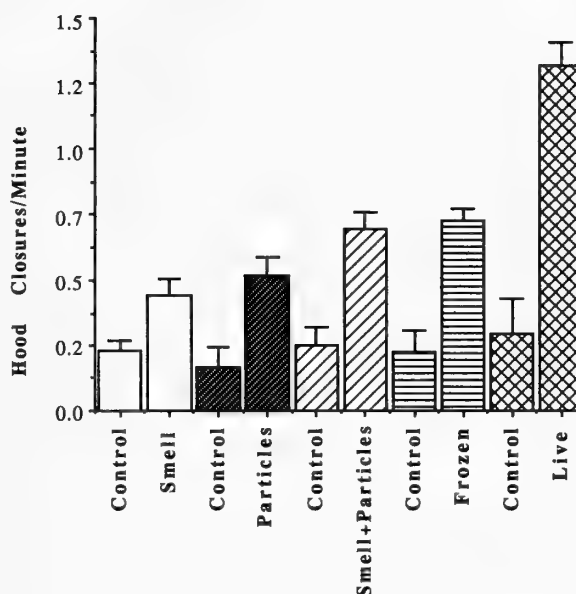


Figure 1

The influence of olfactory and tactile stimuli on the feeding frequency of *Melibe*. Five separate experiments are depicted in this figure, each with separate controls. In the first experiment animals were exposed to *Artemia*-conditioned water (smell), in the second Sephadex beads (particles), the third particles soaked in *Artemia*-conditioned water, the fourth frozen *Artemia*, and in the final experiment animals were exposed to live *Artemia*. In all cases we observed a significant increase in their rate of hood closures following the addition of one of the stimulants. Bars represent standard error of measurement.

often prematurely terminate feeding cycles if food is not present. We also observed this phenomenon in our experiments. When animals were stimulated to feed with an olfactory stimulus they increased their hood closure rate, but they rarely completed a feeding cycle; more than 70% of the feeding cycles they initiated ended before reaching the final consumption phase (Figure 4). This proportion of incomplete episodes was comparable to that observed in controls; however, the feeding movements of control animals are much less frequent and regular. In contrast, all the treatments that provided something to consume, whether inert or otherwise, resulted in a high proportion of complete feeding cycles, and consumption of the objects. As in our other experiments, live prey were the most effective stimuli. Therefore, it appears as if the type of stimuli present influence both the rate of food capture and the sequential expression of movements associated with food acquisition and consumption.

Adult *Melibe* are normally found in eelgrass beds or kelp forests, where they feed on epifaunal crustaceans, or planktonic crustaceans such as copepods and nauplii. Like most gastropods their vision is limited and therefore they must rely heavily on olfaction and mechanoreception to locate food and discriminate appropriate prey from other objects. Our laboratory studies indicate that *Melibe* is sim-

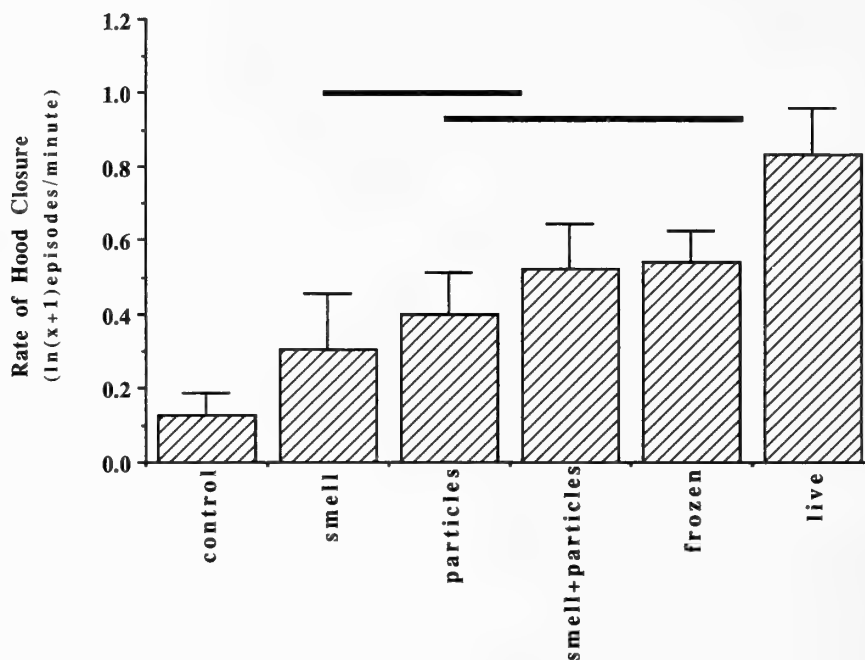


Figure 2

The relative potency of various feeding stimulants. Overall, the treatments were significantly different from each other (ANOVA $F = 44.133$, $df: 5, 54$, $P > 0.0001$). Horizontal lines indicate treatments that are not statistically significant from each other, using the Student-Newman-Keul's multiple comparison test. Both olfactory and tactile stimuli enhance feeding frequency to a limited extent, but neither stimulus alone, or when combined with each other (smell and particles, frozen *Artemia*), are as effective as live animals. The data were transformed using the natural log of $(x + 1)$. Bars represent standard error of measurement.

ilar to other gastropods in their use of chemoreceptors to initiate appetitive aspects of feeding such as changes in locomotion and orientation toward the source of food (KUPFERMANN, 1974; CROLL, 1983; AUDESIRK & AUDESIRK, 1985; TEYKE *et al.*, 1992). It has been suggested that chemical stimuli serve primarily to evoke a food-induced state of arousal in *Aplysia* (KUPFERMANN *et al.*, 1991), and it may serve a similar role in *Melibe* as well. Chemical stimuli cause *Melibe* to change their rate of locomotion, orient toward the source of the stimuli, and increase their rate of feeding movements. However, it appears as if they are merely sampling the water, not feeding, because they do not carry out complete feeding cycles. This increase in the frequency of hood movements may also serve to enhance the ability of putative chemoreceptors on the oral veil to detect prey; comparable to antennule flicking in many crustaceans. Then, once preylike objects make contact with the oral hood, they are captured and brought in contact with the mouth, and normal feeding behavior is initiated.

Most opisthobranchs are well endowed with chemo- and mechanoreceptors (CROLL, 1983) and it has been postulated that these two groups of receptors converge on neurons which regulate different aspects of feeding (ROSEN *et al.*, 1982). Evidence from *Tritonia* also indicates that some mechanoreceptors receive direct input from chemorecep-

tors which modulates their responsiveness (AUDESIRK & AUDESIRK, 1980a), as well as input from some aspect of the swim circuit (AUDESIRK & AUDESIRK, 1980b). Thus a certain amount of integration and discrimination appears to take place very early in the circuit which links sensory input to the feeding circuit, and as a result the presence of certain odors can have an important impact on the responsiveness of the animal to tactile stimulation. This appears to be the case in *Aplysia* (ROSEN *et al.*, 1982) and certain other gastropods, where the biting response to mechanical stimuli is limited unless a chemical cue is also present. In some cnidarians chemical cues actually alter the tuning properties of mechanoreceptors involved with prey capture. WATSON & HESSINGER (1989) found that the receptors controlling the discharge of sea anemone nematocysts are activated by 30–75 Hz vibrations and the chemical cues associated with prey modulate these receptors so they shift their sensitivity to a range of 5–40 Hz, which precisely matches the swimming movements of their prey (they also used *Artemia* in their study). In our experiments it was clear that live *Artemia* stimulated feeding much more effectively than any combination of odor and touch. We are presently searching for receptors in *Melibe* that are most sensitive to the vibrations produced by swimming prey. The possibility that these receptors are also

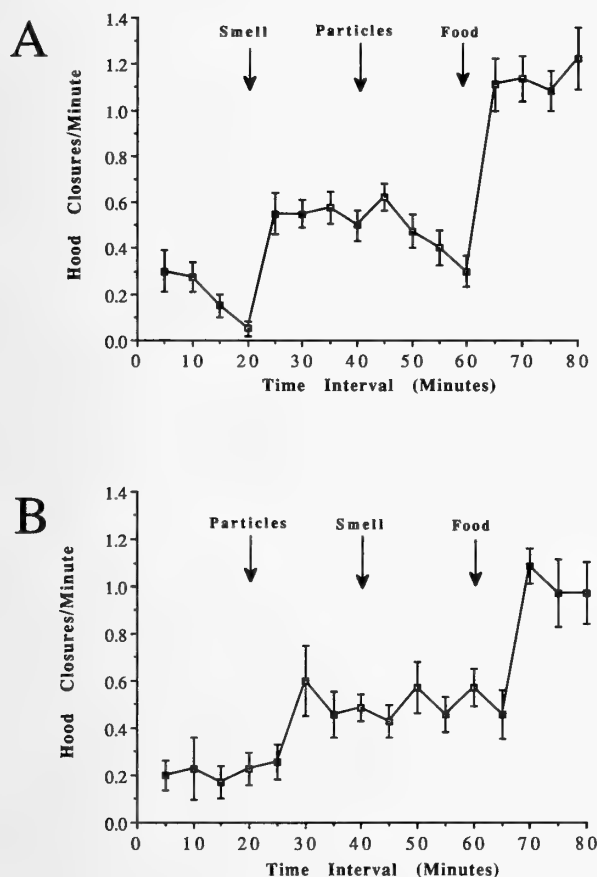


Figure 3

The response of *Melibe* to sequential addition of olfactory and tactile stimulants. A. After 20 min in filtered seawater, conditioned water (smell) was added to the observation tank, resulting in a rapid increase in feeding frequency, which was maintained for 20 min. Addition of particles did not cause any further increase in feeding rate during the next 20 min. However, live prey (food) had a much greater effect on feeding than the combination of particles and food odor. B. This experiment was similar to the one described in A, except particles were added first, followed by smell, and then live prey (food). As in A, addition of a second feeding stimulant did not cause any additional increase in feeding rate, while live prey did. Bars represent standard error of measurement.

modulated by the odor of prey, or the behavioral state of the animals, is also a subject worthy of further investigation.

The stereotyped, rhythmic movements involved in *Melibe* feeding behavior have characteristics typical of fixed action patterns that are under the control of a central pattern generator or motor program (AJESKA & NYBAKKEN, 1976; WATSON & TRIMARCHI, 1992). This motor program is expressed at a very low frequency (0.2 cycles/min) even in the absence of prey, and when it senses prey, through a combination of the cues discussed in this paper, the

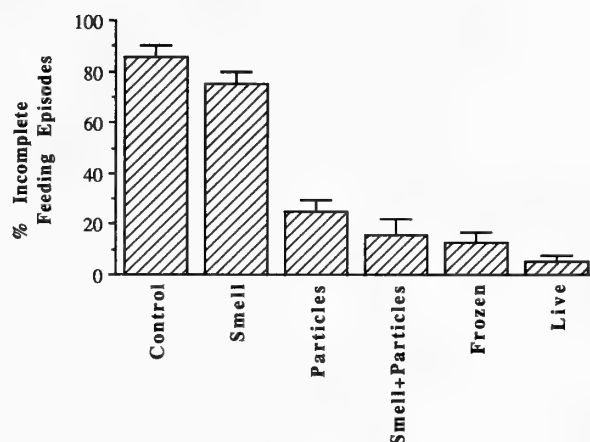


Figure 4

The influence of feeding stimulants on the sequential expression of *Melibe* feeding movements. The typical *Melibe* feeding cycle consists of a series of movements designed to capture prey and bring them in close proximity to the mouth for consumption. If prey are sparse or absent, animals often terminate a feeding cycle before the tilt and squeeze phase of the cycle, which brings food to the mouth. This figure shows the proportion of such prematurely terminated feeding cycles during different treatments. It is clear that while the odor of prey stimulates feeding activity (Figures 1, 2), the type of feeding movements displayed are seldom complete. In contrast, when any type of particle is present, animals usually attempt to engulf the objects they capture, resulting in complete feeding cycles.

cycling rate of the motor program increases. In addition, the quality and quantity of sensory input appear to influence the full expression or completeness of the feeding cycle. If only the odor of food is present, animals become aroused and sample the water column for food, often terminating their feeding cycle prior to making the movements that normally bring prey in close proximity to the mouth. However, if particles are present, or live prey, most feeding cycles are complete. We hypothesize that *Melibe* feeding behavior consists of a series of flexible motor programs that are centrally programmed, triggered by sensory input, and modulated by sensory feedback throughout the feeding cycle. This hypothesis is derived, in part, from an emerging view of central pattern generators as broader more flexible motor pattern networks, which combine elements of traditional motor programs with a high level of sensory modulation (HARRIS-WARRICK & Johnson, 1989). Our present studies are designed to test this hypothesis and examine this relatively new view of "stereotyped" behavior.

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Ecological, Morphological, and Genetic Differences Between the Sympatric Bivalves *Donax variabilis* Say, 1822, and *Donax parvula* Philippi, 1849

by

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Abstract. To clarify the status of *Donax variabilis* Say, 1822, and *D. parvula* Philippi, 1849, as separate species, comparisons of measurements of shell characteristics, spatial distribution patterns, and allozyme frequencies were made on sympatric populations from Melbourne Beach, Florida, USA. A significant difference in the regression slopes of shell width versus shell height was found, although there was overlap in the data for most of the size range of the specimens examined. The angle of the dorsal margins of the shell immediately anterior and posterior to the umbo provided a clear separation of the species. Marked differences in frequencies of alleles, but no unique alleles, were found for the two species. While *D. parvula* tended to be distributed more subtidally than *D. variabilis*, this pattern varied with season and there was little spatial separation of the species particularly during spring and fall. The balance of evidence indicates that *D. variabilis* and *D. parvula* are separate, but highly similar species.

INTRODUCTION

The taxonomy of the species of the genus *Donax* along the Atlantic coast of the United States was revised by MORRISON (1971). Within the region from Ocracoke, North Carolina, to St. Lucie County, Florida, Morrison recorded two sympatric species, *Donax variabilis* Say, 1822, and *Donax parvula* Philippi, 1849. *Donax variabilis* has a greater range, extending from the coast of Virginia to the coast of Mississippi. Following the taxonomic divisions of MORRISON (1971), a western subspecies, *D. variabilis roemeri* Philippi, 1849, continues from the Mississippi delta to Campeche, Mexico. In spite of Morrison's revision, some authorities

have not recognized the specific status of *D. parvula* (ABBOTT, 1974; DANCE, 1990), considering *D. parvula* to be merely an ecomorph of *D. variabilis* (R. T. Abbott, personal communication).

As MORRISON (1971) and MIKKELSEN (1985) point out, studies of the growth rates of *Donax* in the south Atlantic may have been complicated by the possible presence of two species in the samples used for analysis. Similar problems of interpretation exist for some early studies of tidal migration behavior (TURNER & BELDING, 1957) and recruitment patterns (PEARSE *et al.*, 1942). The present paper presents data on the spatial distribution patterns, mor-

Table 1

Electrophoretic methods used. Allozyme abbreviations are explained in the text.

Allozyme	Number of loci	Poly-morphic	Buffer	Buffer no. (WERTH, 1985)
ACPH	1	no	tris-citrate pH 8	7
GOT	1	no	tris-citrate pH 8	7
IDH	1	no	morpholine pH 6.5	1
LAP	1	yes	lithium hydroxide	3
MDH	2	no	morpholine pH 6.5	1
ME	1	no	morpholine pH 6.5	1
6-PGD	1	yes	morpholine pH 6.5	1
GPI	1	yes	tris-citrate pH 7	8
PGM	1	yes	tris-citrate pH 8	7

phometrics, and allozyme frequencies for *D. variabilis* and *D. parvula* from Melbourne Beach, Florida, to resolve the species issue.

MATERIALS AND METHODS

Collections of *Donax* were made at approximately monthly intervals between February 1982 and August 1983 on a moderately exposed sand beach at Melbourne Beach, Florida, at Florida Department of Natural Resources coastal construction survey marker R-140 (28°2'55"N, 80°34'54"W). Details of the sampling site and sampling methods are given in BONSDORFF & NELSON (1992).

Four replicate 20.3-cm-diameter cores were taken at the high tide line, the base of the swash zone, and at 61 and 91 m from the high tide line. Water depths at the 61- and 91-m sites were in the range 1.5–3 m. All samples were sieved in the field on a 0.5-mm-mesh screen, fixed in 10% formalin, resieved on a 0.5-mm screen in the laboratory, and preserved.

All *Donax* were identified under a dissecting microscope. Small individuals (<3 mm) could not always reliably be assigned to one species, and most were classed as *Donax* spp.

The subsamples used for morphometric analysis were identified by Mr. Paul Mikkelsen, who has experience with these *Donax* species (MIKKELSEN, 1978, 1981, 1985), following the guidance of MORRISON (1971). Photographs of both species are available in MORRISON (1971: pl. 1, 2). Voucher specimens were deposited in the Harbor Branch Oceanographic Museum, Fort Pierce, Florida (*D. parvula*, Catalog Nos. HBOM 064:01965, HBOM 064:01966, HBOM 064:01967; *D. variabilis*, Catalog Nos. HBOM 064:01968, HBOM 064:01969).

Length, height and width of each shell were measured with an optical micrometer. Linear regression equations were computed relating shell length, height, and width from subsamples of both species. Data sets were checked for homogeneity of variances with the F_{\max} -test. Analysis

Table 2

Regression equations relating shell measurements for *Donax variabilis* and *D. parvula* with Analysis of Covariance results, where appropriate.

Comparison	Equation	F value (slopes)
Width vs. length		
<i>D. variabilis</i>	$y = 0.51x - 0.42$	(1)
<i>D. parvula</i>	$y = 0.62x - 0.63$	
Width vs. height		
<i>D. variabilis</i>	$y = 0.91x - 0.78$	4.68; $P < 0.05$
<i>D. parvula</i>	$y = 1.10x - 1.00$	
Height vs. length		
<i>D. variabilis</i>	$y = 0.58x + 0.01$	(1)
<i>D. parvula</i>	$y = 0.53x + 0.63$	

(1) Variances heterogeneous; no test possible.

of covariance (SOKAL & ROHLF, 1981) was used to compare the regression equation between the two species for data sets with homogeneous variances.

From the above subsamples, 20 specimens of each species were oriented horizontally with the left valve down, and the dorsal margin of the shell immediately anterior and posterior to the umbo was traced with the aid of a camera lucida. The angle between the anterior and posterior shell margins of the drawing was then measured with a protractor.

On 29 April 1990 specimens of *Donax variabilis* and *D. parvula* were collected from the same Melbourne Beach study site and sorted live. The clams were placed in plastic vials, packed with dry ice, and transported to George Mason University for allozyme analysis. All allozymes were visualized using starch gel electrophoresis (WERTH, 1985). The enzymes examined and the buffers used are listed in Table 1.

RESULTS

Morphometric Comparisons

The regression equations relating shell width and shell length, shell width and shell height, and shell height and shell length for both species of *Donax* are given in Table 2. For width versus length and height versus length, two-tailed F -tests (SOKAL & ROHLF, 1981) indicated heterogeneity of variances between species. Transformation did not resolve this problem, and therefore no analysis of covariance is presented. In both cases, slopes of the regression lines were similar.

The heterogeneous variances may be due to the inclusion of a much larger range of sizes (primarily large individuals) of *Donax variabilis* compared to *D. parvula*. The lack of larger *D. parvula* does not appear to be solely an artifact of the subsample. Individuals in the size range of 7–8 mm

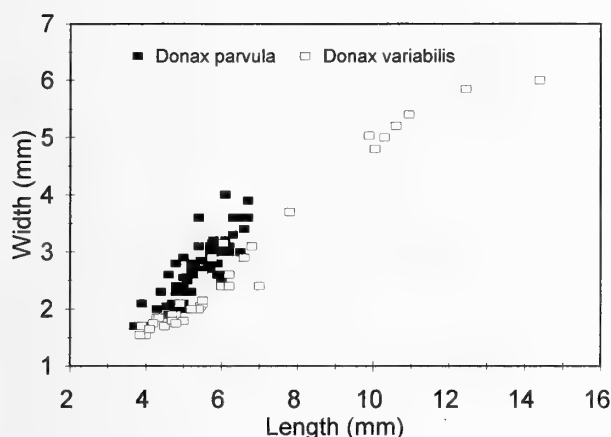


Figure 1

Scattergrams of shell width (mm) vs. shell length (mm) for *Donax variabilis* and *D. parvula* (regressions given in Table 2) illustrating the overlap in morphometric distributions.

were relatively common in some months, but were not represented in the subsample. However, while the largest specimen of *D. parvula* collected in 16 months of sampling was approximately 12 mm, individuals larger than 8 mm were rarely recorded (BONSDORFF & NELSON, 1992). Adult shell size in *D. parvula* is truly smaller than it is in *D. variabilis*.

Some overlap in the relationship of shell width versus shell length exists for *Donax variabilis* and *D. parvula* (Figure 1). Analysis of covariance indicated that the slopes of the lines relating shell width and shell height for the two *Donax* species are significantly different (Table 2, Figure 2), with width increasing more rapidly for a given height increase in *D. parvula*. Overlap of shell width and shell height relationships for the two species was also present.

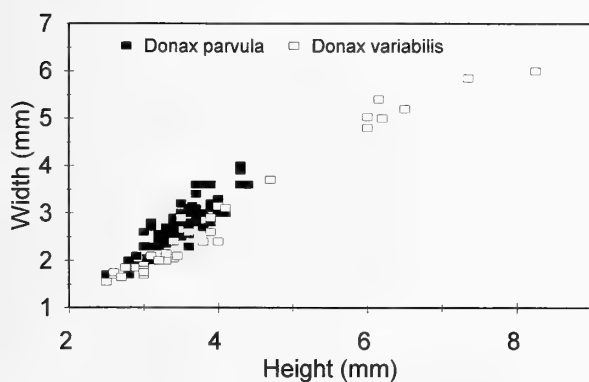


Figure 2

Scattergrams of shell width (mm) vs. shell height (mm) for *Donax variabilis* and *D. parvula* (regressions given in Table 2) illustrating the overlap in morphometric distributions.

Table 3

Allele frequencies for *GPI* and *PGM* in *Donax* species.

<i>GPI</i> allele	<i>D. variabilis</i> (n = 101)	<i>D. parvula</i> (n = 89)
1	0.0099	0.0225
2	0.0891	0.4663
3	0.8366	0.4944
4	0.0644	0.0169
<i>PGM</i> allele	<i>D. variabilis</i> (n = 77)	<i>D. parvula</i> (n = 76)
1	0.0519	0.0066
2	0.7078	0.0921
3	0.2338	0.8421
4	0.0065	0.0592

Measurement of the angle between the anterior and posterior dorsal shell margins in the vicinity of the umbo clearly separated the two species. The mean shell angle for *Donax parvula* was 120.9° while that for *D. variabilis* was 131.4°, a highly significant difference (*t*-test, *t* = -8.76, *P* < 0.001). There was no significant relationship of shell angle to total shell length for *D. parvula*, whereas the regression of these variables showed a significant positive relationship for *D. variabilis* ($y = 1.02x + 119.29$, *t* = 3.37, *P* < 0.01).

Allozyme Comparisons

On the basis of a sample of 20 individuals per species, the genes for acid phosphatase (*ACPH*), glutamate oxaloacetate transaminase (*GOT*), isocitrate dehydrogenase (*IDH*), malate dehydrogenase (*MDH*), and malic enzyme (*ME*) were monomorphic and showed no differences between the two species. Leucine aminopeptidase (*LAP*) and 6-phosphogluconate dehydrogenase (*6-PGD*) were definitely polymorphic, but the resolution of their allozymes was poor, especially in *Donax parvula*, and allele frequencies were not considered to be reliable. Only the allozymes for phosphoglucosmutase (*PGM*) and glucose phosphateisomerase (*GPI*) were both polymorphic and easily scorable. These genes were examined in larger samples, and the loci did distinguish between the two taxa. Although all of the alleles were present in both species, the patterns of allele frequencies were clearly different. For the gene *PGM*, species differed in major allele, while for *GPI*, *D. variabilis* had a majority allele and *D. parvula* did not (Table 3).

The differences between the two taxa for both *GPI* and *PGM* were highly significant (*GPI*, *P* < 0.001; *PGM*, *P* < 0.001; *G*-test of independence, SOKAL & ROHLF, 1981). Within each species, genotype frequencies for each locus were tested for conformance to Hardy-Weinberg expectation using the chi-square statistic. Because of the large number of possible genotypes (10 for each locus) and the small expectations for some of them, all but the two most common genotypes (or for *GPI* in *Donax parvula*, the three

Table 4

Spatial distribution patterns of numerical abundance of *Donax parvula* and *D. variabilis* at Indialantic and Melbourne Beach, Florida. Data are mean number per m² (15 cm diameter core, $n = 3$) for all three study sites of SPRING (1981).

Season	Distance from the high tide line (m)					
	0	5	27	55	73	91
<i>Donax parvula</i>						
Summer	11.3	73.4	197.8	401.1	339.0	175.1
Fall	0.0	0.0	5.6	11.3	56.5	118.6
Winter	0.0	0.0	0.0	33.9	11.3	45.2
Spring	0.0	0.0	33.9	169.5	231.6	141.2
Composite	2.8	16.9	56.5	152.5	158.2	124.2
<i>Donax variabilis</i>						
Summer	84.7	118.6	638.4	779.7	225.0	11.3
Fall	790.9	73.4	90.4	113.0	84.7	101.4
Winter	5.6	50.8	0.0	124.3	62.2	67.8
Spring	519.8	474.6	56.5	50.8	52.5	33.9
Composite	350.3	180.8	197.7	265.5	101.6	50.8
<i>Donax</i> spp. (<3 mm)						
Summer	203.4	412.4	2740.1	2858.7	84.7	1446.3
Fall	0.0	0.0	1446.3	5124.3	2711.4	1983.0
Winter	0.0	0.0	45.2	870.1	502.8	1446.3
Spring	0.0	0.0	627.1	1791.0	1101.7	113.0
Composite	50.8	101.6	1214.6	2661.0	1096.0	1242.9

most common), were pooled into a single class for the statistical test. None of the deviations from Hardy-Weinberg was significant ($P \geq 0.05$).

Spatial Distribution Patterns

SPRING (1981) sampled three locations quarterly (including R-140) off Indialantic and Melbourne Beach, Florida, during 1979 and 1980. A detailed breakdown of Spring's original data indicates some evidence of spatial separation of *Donax variabilis* and *D. parvula*, and of seasonal changes in the degree of separation (Table 4). During fall and spring, *D. variabilis* was relatively more abundant inshore and *D. parvula* was found in relatively greater abundances offshore. During the summer, maxima of both species were found at the same location subtidally at intermediate distances from the shore (27–55 m from high tide line). During winter, density maxima of both species were found offshore (55–91 m from high tide). Small individuals of the two species (combined for this analysis) tended to have a maximum density offshore at all seasons, with the maximum more seaward during the winter (Table 4). At all seasons, distributions of both species were broadly overlapping.

The spatial distribution patterns of the two species based on the more extensive collections in the present study indicate somewhat different patterns from those found in Spring's collections. *Donax variabilis* was relatively more

Table 5

Spatial distribution patterns of numerical abundance of *Donax parvula* and *D. variabilis* at Melbourne Beach, Florida. Data are mean number per m², with $n = 3$ months of samples for summer and fall and $n = 4$ and 6 for winter and spring, respectively.

Season	Distance from the high tide line (m)			
	0	Swash zone	61	91
<i>Donax parvula</i>				
Summer	0.0	41.7	293.3	290.7
Fall	0.0	259.0	397.3	124.3
Winter	0.0	393.0	101.3	89.5
Spring	0.0	26.0	79.2	90.8
Composite	0.7	179.9	217.8	148.8
<i>Donax variabilis</i>				
Summer	0.0	85.6	757.6	163.0
Fall	10.3	59.7	29.8	122.3
Winter	2.0	52.9	140.3	552.6
Spring	17.5	31.0	1074.3	399.6
Composite	7.5	57.3	500.5	309.4
<i>Donax</i> spp. (<3 mm)				
Summer	2.7	5.3	2155.0	324.0
Fall	0.0	44.6	844.0	7245.0
Winter	0.0	0.0	115.0	387.0
Spring	0.0	0.0	1462.0	1092.0
Composite	0.7	11.7	6004.0	2262.0

abundant at offshore locations (61–91 m) at all seasons (Table 5). *Donax parvula* tended to be found offshore during spring and summer, and tended to move inshore during fall and winter. The density maxima for both species were generally in the same subtidal region for three seasons, showing some separation during winter. Thus the degree of spatial separation shown by the two species was less than shown in SPRING's (1981) data (Table 4). Small *Donax*, as Spring found, had much greater abundances at the offshore stations at all seasons (Table 5).

DISCUSSION

Morphometric and Genetic Characteristics

According to MORRISON (1971), one of the morphological features for distinguishing between *Donax variabilis* and *D. parvula* is the relative width of shells. While significant difference in the regression of shell width versus shell height was found, that between shell width and length could not be statistically evaluated. Scatter plots of both pairs of variates (Figures 1, 2) showed that there is some overlap for most of the size range of the specimens examined. This was particularly true for smaller individuals. The situation with regard to sympatric *D. variabilis* and *D. parvula* in terms of morphometric overlap of shell width versus length differs from a case examined by ANSELL (1983b) for four species of *Donax* occurring in Hong Kong.

Three of four species showed no overlap for scattergrams of shell width versus length. One species showed total overlap of these parameters with a second species, but the species were not recorded sympatrically.

Separation of *Donax variabilis* and *D. parvula* on the basis of relative shell width alone is difficult. Shell shape is known to be extremely variable in some *Donax* species (WADE, 1967; ANSELL, 1983a). MORRISON (1971) stated that "the posterior slope of *D. parvula* is glossy and not externally radially ribbed" as is the case for *D. variabilis*. However, this character also appears to be undeveloped for very small specimens.

Measurement of the angle between the anterior and posterior dorsal margins of the shell in the vicinity of the umbo gave a clear separation between the two species. Using the photographs of the two species in MORRISON (1971: pl. 1, 2), measurements of shell angle gave values virtually identical to the mean values reported here. More detailed studies of the morphology of these two species, including soft tissues, may provide additional characters for accurate separation of these species in ecological studies. This is particularly needed for the smallest specimens, which may be numerically dominant in quantitative collections (BONSDORFF & NELSON, 1992).

Genetic differences in allozymes do not definitively separate the two species. No fixed differences between the two species were found among the invariant loci and no unique alleles were detected among the variable genes. However, because the two species are broadly sympatric, it is likely that their gene pools are separate. Differentiation in allele frequencies to the extent found in this study is not likely when hybridization is more than a rare occurrence, but, in the absence of genetic markers unique to one species, the possibility cannot be excluded.

On the bases of shell morphology and allozymic frequencies, *Donax variabilis* and *D. parvula* present a case intermediate among situations reported for *Mytilus*, *Macoma*, and *Mercenaria*. KOEHN *et al.* (1984) found a similar level of allozymic differentiation among allopatric populations of the blue mussel *Mytilus edulis*, but reported no morphological differences. They nevertheless considered the differences great enough to raise a suspicion that cryptic, unrecognized species existed in the northern Atlantic. Because the putative species in their study were not sympatric, the possibility of interbreeding could not be assessed.

MEEHAN (1985) found little morphological differences among populations of *Macoma balthica* from the eastern and western Atlantic, although genetic similarity values between these populations were sufficiently low for them to be considered separate species. Differences among populations included both unique alleles and large differences in allele frequencies.

In a comparison of the hard clams *Mercenaria mercenaria* and *M. campechiensis*, DILLON & MANZI (1989) found comparable morphological, and greater allozymic, differentiation than reported here for *Donax variabilis* and *D.*

parvula. Although they also did not report fixed differences in alleles for the loci examined, they did find 15 alleles that were unique to one or the other species. When they examined clams from a mixed population, they found convincing genetic and morphological evidence for hybridization, a situation that cannot yet be assessed in *Donax*.

Spatial Distribution

ANSELL (1983a) commented that in general, where more than one species of *Donax* occurs within an area, there is little habitat overlap between the species. MORRISON (1971) observed complete spatial separation of *D. variabilis* and *D. parvula* on a wide beach in South Carolina, and a high degree of separation has been observed for these species near Jacksonville Beach, Florida (the type locality for *D. parvula*), where the beach also tends to be broad with a low slope (P. S. Mikkelsen, personal communication). MORRISON (1971) described *D. variabilis* as living intertidally throughout the year, with part of the population often remaining in mid-intertidal areas during low tide.

Complete spatial separation of *Donax variabilis* and *D. parvula* does not invariably occur. LEBER (1982) found that on the coast of North Carolina these species migrated together in the swash zone from January through July. In August, *D. parvula* disappeared from the intertidal zone and Leber suggested that it had migrated seaward to 1 m depth in the surf zone. *Donax variabilis* ceased tidal migrations in August and remained high on the beach in damp sand. Both species had disappeared from the intertidal by December, and recolonized the beach in the following March. Leber did not regularly sample the subtidal area, and thus what may have occurred subtidally is unclear.

At Melbourne Beach, which has a fairly steep slope and high energy, there was never a clear spatial separation of the two species. These collections do not support MORRISON's (1971) suggestion that *Donax variabilis* is mainly an upper intertidal species. Both *D. variabilis* and *D. parvula* were maximally abundant at the offshore, subtidal locations at the Melbourne Beach site. MATTA's (1977) work in North Carolina, in an area believed to be north of the distributional limit of *D. parvula*, recorded *Donax* spp. (presumably *D. variabilis* or possibly *D. fossor*) as concentrated all year subtidally at 30–60 m distance from the high tide line. Distribution of small individuals was similar to that found in the present study.

Local differences in abundance along a beach gradient may be affected not only by the tides (TURNER & BELDING, 1957) and seasons (LEBER, 1982), but also by beach morphology (DONN *et al.*, 1986). Local differences in organic input to beaches have also been shown to influence population characteristics of a *Donax* species (SASTRE, 1984). Therefore, it may be found that the spatial distribution patterns of *D. variabilis* and *D. parvula* may be variable from site to site.

The distribution pattern of two species from the Texas

coast, *Donax variabilis roemeri* and *D. texasianus* Philippi, 1847, showed similarities to the situation in North Carolina in that complete spatial separation occurred at some, but not all, times of the year (VEGA & TUNNELL, 1987). *Donax v. roemeri* occurred intertidally and *D. texasianus* occurred subtidally from February until April. At least a portion of the population of both species migrated tidally during May to August.

With the exceptions of the present study and of MATTA's (1977) work from North Carolina, the majority of studies of *Donax* on the Atlantic coast have almost exclusively sampled in the intertidal zone (e.g., MIKKELSEN, 1981; LEBER, 1982; ADAMKEWICZ, 1989). On the central Florida coast, a substantial portion of both *D. variabilis* (93%) and *D. parvula* (67%) were found subtidally, even when individuals were also present in the intertidal (BONSDORFF & NELSON, 1992). For individuals <3 mm in length, 99.9% of all *Donax* were found subtidally. In Texas, VEGA & TUNNELL (1987) showed that 15% of *Donax v. roemeri* and 85% of *D. texasianus* were found subtidally. Failure to account for the subtidal portion of the population in studies of *Donax* will clearly lead to a highly biased description of population characteristics.

ACKNOWLEDGMENTS

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New Reports of the Large Gastropod *Campanile* from the Paleocene and Eocene of the Pacific Coast of North America

by

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Abstract. The Old World Tethyan prosobranch gastropod genus *Campanile* Fischer, 1884, is reported from six new localities in California. Three of these new reports are for the late Paleocene *C. greenellum* Hanna & Hertlein, 1939, with two localities in the Santa Susana Formation, Santa Monica Mountains, southern California, and a locality in the San Francisquito Formation, Redrock Mountain area near Castaic Lake, southern California. These are the first reports of *C. greenellum* from southern California. The three other new reports are for the early Eocene *C. dilloni* Hanna & Hertlein, 1949, with localities in both the Santa Susana and Lajas Formations, Bus Canyon, south side of Simi Valley, southern California, and a locality in the Sierra Blanca Limestone near Oso Canyon, Santa Ynez River Valley, southern California.

A previously known Paleocene *Campanile* sp. in an unnamed mudstone in the northern Santa Lucia Range, central coastal California, is herein identified as *Campanile* sp. indet. *Campanile* sp. Nelson, 1925, from the Sierra Blanca Limestone near Lake Cachuma, southern California, is herein identified as *C. dilloni*.

INTRODUCTION

The gastropod genus *Campanile* Fischer, 1884, has a geologic range from Late Cretaceous (Maastrichtian) to Recent (WENZ, 1940). The genus is best known from the Paris Basin Eocene fauna where well-preserved specimens of *C. giganteum* (Lamarck, 1804), up to a meter in length, are known from middle Eocene (Lutetian) strata of Damerly near Epernay, France. These specimens, and some of about the same size from Jamaica (JUNG, 1987), are among the largest gastropods of all time.

During the early Tertiary, *Campanile* underwent a geographic expansion. Many species lived in the Old World Tethys Sea, but some migrated westward. The distribution of known occurrences of early Tertiary *Campanile* extends in a band from northwest India through France, to Alabama and the Caribbean area, and on into Baja California Sur, Mexico, and California. *Campanile* was an Old World Tethyan genus that immigrated into North America during the Paleogene (GIVENS, 1989). *Campanile* arrived in California during the Paleocene (SQUIRES, 1984). Only a single species, *C. greenellum* Hanna & Hertlein, 1939, is known, and it has been found at a few localities in northern

California. It is characterized by a wide pleural angle (approximately 35°), numerous wide nodes (approximately 22) on the carina in the posterior part of the whorls, and three spiral ribs anterior to the carina. I report here three new localities for this rare species from upper Paleocene strata in southern California.

During the early Eocene, which was the warmest time of the Cenozoic (HAQ, 1981), *Campanile* attained its maximum geographic distribution for the Pacific coast region of North America. Only a single species, *C. dilloni* Hanna & Hertlein, 1949, is known, and it has been found at several localities from southern to south-central California. It is characterized by a relatively narrow pleural angle (approximately 20°), approximately 8 to 16 nodes on the carina in the posterior part of the whorls, and three to four spiral ribs anterior to the carina. I report here three new localities for this rare species from lower Eocene strata in southern California.

By middle Eocene time, *Campanile* disappeared from the Pacific coast region of North America. On a worldwide basis, after the middle Eocene, there was a sharp decrease in the species diversity of *Campanile*. Neogene and Pleis-

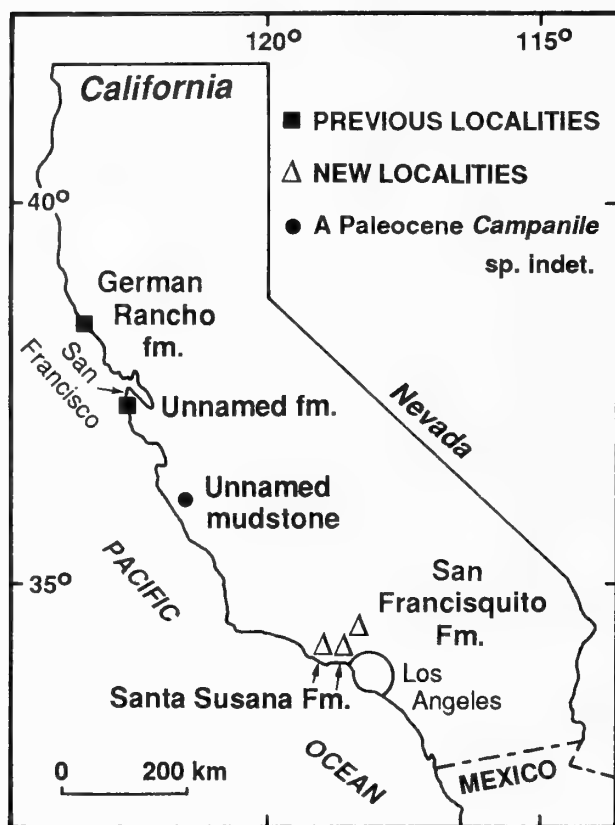


Figure 1

Index map of previous and new localities of *Campanile greenellum* Hanna & Hertlein, 1939.

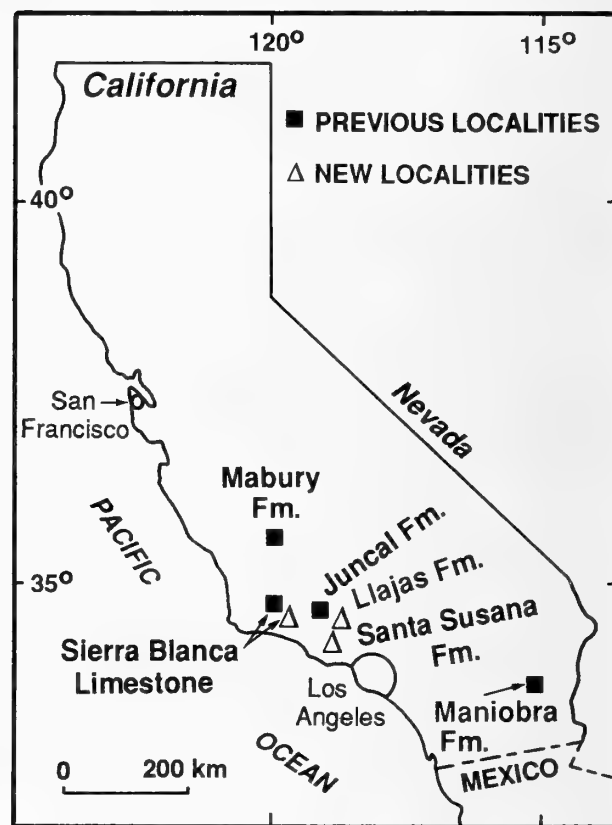


Figure 2

Index map of previous and new localities of *Campanile dilloni* Hanna & Hertlein, 1949.

tocene records are scarce, and the sole surviving species is *C. symbolicum* Iredale, 1917, which lives in large populations on sandy patches between rocks in depths of 1 to 4 m along the southwestern coast of Australia (HOUBRICK, 1984).

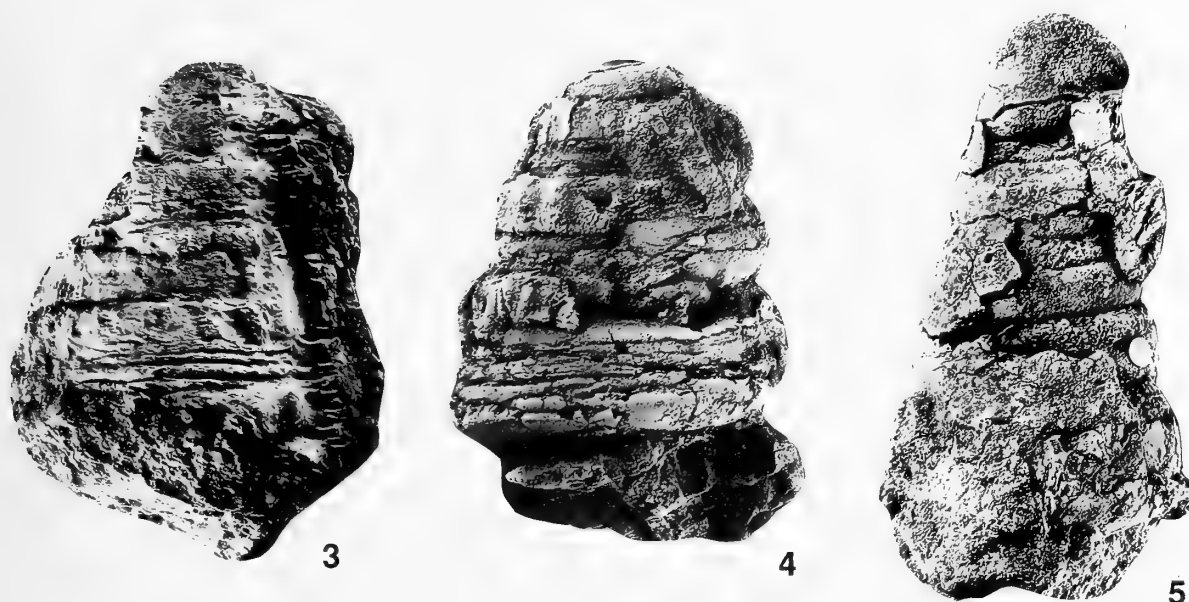
The term "Martinez Stage" used in this report has had a complex nomenclatural history and a variable geologic age assignment since first introduced as a concept by early workers in the 1860s (CLARK & VOKES, 1936). Workers now assign this provincial stage to the late Paleocene (SAUL, 1983a:fig. 1; ZINSMEISTER, 1983). The terms "Meganos Stage" and "Capay Stage" used in this report stem from CLARK & VOKES (1936), who informally proposed Pacific coast of North America provincial megainvertebrate Eocene stages. The "Meganos Stage" has been refined by SAUL (1983a) to be latest Paleocene to early Eocene in age, and the "Capay Stage" has been refined by GIVENS (1974) to be restricted to the middle early Eocene. These refinements are summarized in SQUIRES (1988) and are used here.

Abbreviations used for catalog and/or locality numbers are: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County,

Invertebrate Paleontology Section; LSJU, Leland Stanford, Jr., University (collections now housed at the CAS); UCLA, University of California, Los Angeles (collections now housed at the LACMIP); UCMP, University of California Museum of Paleontology, Berkeley.

NEW LOCALITIES OF *Campanile greenellum*

The three new localities of *Campanile greenellum* are from the Los Angeles area, southern California (Figure 1). Two of the localities are from Trailer Canyon in the Santa Monica Mountains at LACMIP locs. 24433 and 27023. DIBBLE (1992) mapped the rocks in the area of the localities as the Santa Susana Formation of Paleocene age. The only fossil found at locality 24433 was a single specimen of *C. greenellum* (Figure 3). It is a well-preserved 7.5-cm-long fragment. The specimen was found in a very fine-grained silty sandstone, rich in fragments of calcareous algae. The only fossil at nearby locality 17023 was a single specimen of *C. greenellum* (Figure 4). It is an internal mold of a 4.5-cm-long fragment of the upper spire, and it shows the diagnostic numerous whorl-shoulder nodes. The specimen was found in micaceous sandstone.



Explanation of Figures 3 to 5

Figures 3–5. *Campanile greenellum* Hanna & Hertlein, 1939. Figure 3. Hypotype LACMIP 12232, LACMIP loc. 24433, Santa Susana Formation, Santa Monica Mountains, abapertural? view, $\times 0.89$. Figure 4. Hypotype LACMIP 12233, LACMIP loc. 27023, Santa Susana Formation, Santa Monica Mountains, apertural view, $\times 1.36$. Figure 5. Hypotype LACMIP 12234, LACMIP loc. 24716, lower San Francisquito Formation, Redrock Mountain, internal mold, abapertural? view, $\times 0.70$.

The third new locality of *Campanile greenellum* is from the lower part of the San Francisquito Formation on Redrock Mountain, near Castaic Lake, at LACMIP loc. 24716. SAUL (1983b:94, 124) assigned the age of the rocks at this locality to the late Paleocene on the basis of the presence of *Turritella peninsularis* Anderson & Hanna, 1935. According to Saul (personal communication), the specimens of *T. peninsularis* at this locality are very close in morphology to *T. peninsularis quaylei* Saul, 1983b, of early Paleocene age. At LACMIP loc. 24716, three internal molds of *C. greenellum* were found. The largest specimen (Figure 5) shows best the diagnostic wide pleural angle and the numerous whorl-shoulder nodes. The specimens were found in coarse-grained sandstone and were associated with numerous specimens of *T. peninsularis*, a few ostreid fragments, and a few other gastropod internal molds.

NEW LOCALITIES OF *Campanile dilloni*

The three new localities of *Campanile dilloni* are from southern California (Figure 2), with two of the localities in Bus Canyon, Ventura County, and the other locality near Oso Canyon, Santa Barbara County.

One of the new localities of *Campanile dilloni* in Bus Canyon is from the uppermost Santa Susana Formation as CSUN loc. 1565. SQUIRES (1991a) assigned the age of the rocks from the same part of the Santa Susana Formation (e.g., the upper 100 m) just east of loc. 1565 to the earliest Eocene ("Meganos Stage"). The only fossil found

at loc. 1565 was the single specimen of *C. dilloni*. It is a well-preserved specimen (Figures 6, 7) found in steel-gray siltstone.

The other new occurrence of *Campanile dilloni* in Bus Canyon is from the lowermost marine part of the Llajas Formation at CSUN loc. 703. The Llajas Formation unconformably overlies the Santa Susana Formation. SQUIRES (1984) assigned the age of the Llajas Formation strata at locality 703 to the middle early Eocene ("Capay Stage"). Although numerous shallow-marine macrofossils were found at this locality, only a single specimen (Figure 8) of *C. dilloni* was found. It is an internal mold, but it is of large size and has a narrow pleural angle. Both of these features help to distinguish this species.

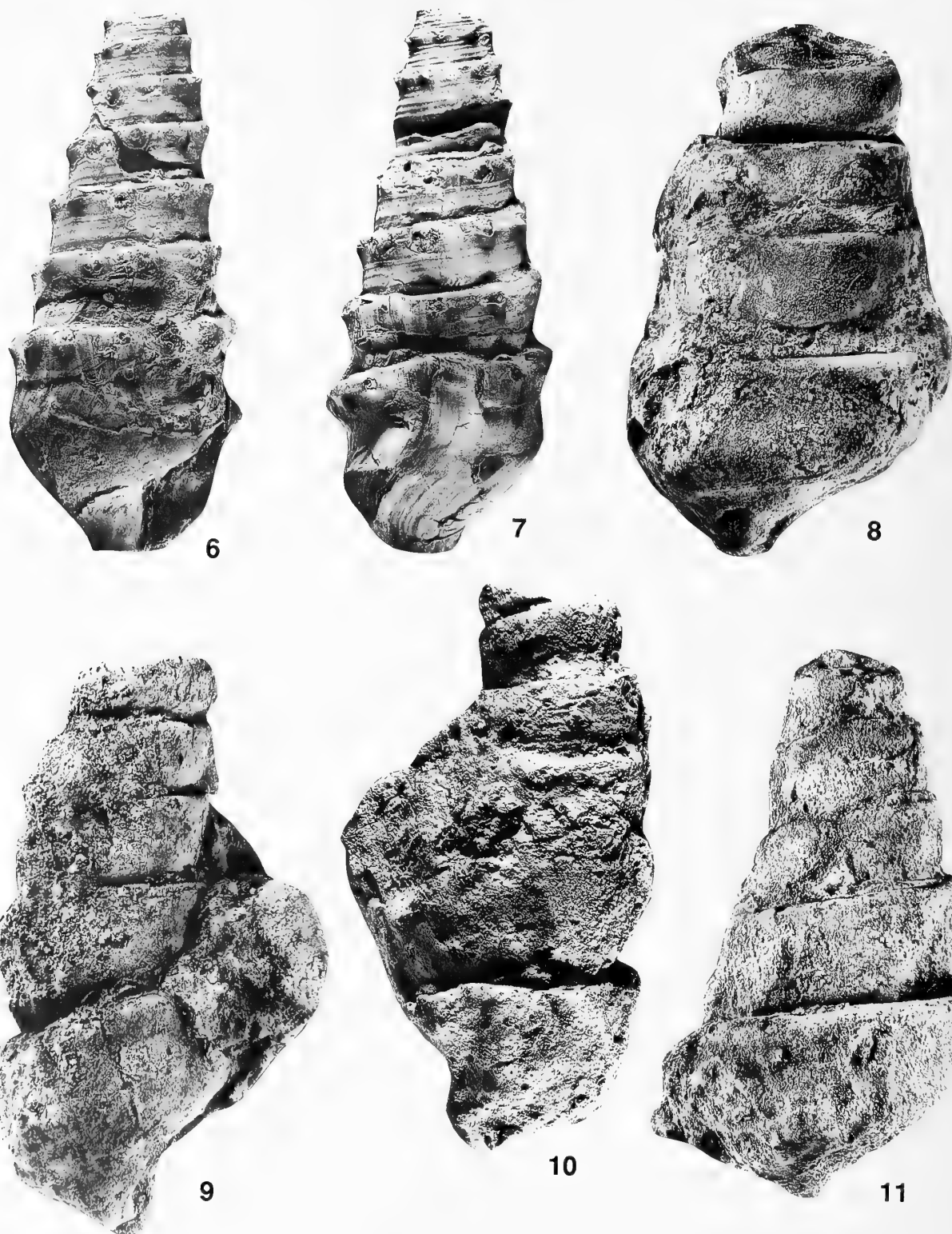
The third new locality of *Campanile dilloni* is from the Sierra Blanca Limestone in the Oso Canyon area, Santa Ynez River Valley, at CSUN loc. 1566. DIBBLEE (1987) assigned the age of the Sierra Blanca Limestone in this area to the early Eocene. Only a single specimen (Figures 9, 10) of *C. dilloni* was found there. It is an internal mold of large size with a narrow pleural angle.

SYSTEMATIC PALEONTOLOGY

Family CAMPANILIDAE Douvillé, 1904

Genus *Campanile* Fischer, 1884

Type species: *Cerithium giganteum* Lamarck, 1804, by subsequent designation, Sacco, 1895; Eocene, Paris Basin, France.



Explanation of Figures 6 to 11

Figures 6-11. *Campanile dilloni* Hanna & Hertlein, 1949. Figures 6, 7. Hypotype LACMIP 12235, CSUN loc. 1565, upper Santa Susana Formation, Bus Canyon, Simi Valley, $\times 0.59$. Figure 6. Apertural view. Figure 7. Abapertural view. Figure 8. Hypotype LACMIP 12236, CSUN loc. 703, Lajas Formation, Bus Canyon, Simi Valley, internal mold, abapertural view, $\times 0.52$. Figures 9, 10. Hypotype LACMIP 12237, CSUN loc. 1566, Sierra Blanca Limestone, near Oso Canyon, Santa Barbara County, internal mold, $\times 0.49$. Figure 9. Apertural view. Figure 10. Abapertural view. Figure 11. Hypotype LACMIP 12238, CSUN loc. 955 = UCMP loc. A-2990, Sierra Blanca Limestone, Lazaro Creek, Santa Barbara County, internal mold, abapertural view, $\times 0.47$.

Remarks: The type species of *Campanile* has been much debated, and the reader is referred to HOUBRICK (1981) and SQUIRES & ADVOCATE (1986) for discussions of the difficulties.

The name *Campanile* was used on the Pacific coast of North America until HANNA & HERTLEIN (1949) used *Campanilopa* Iredale, 1917. WENZ (1940) and HOUBRICK (1981) have pointed out, however, that *Campanilopa* is a junior synonym of *Campanile*.

Recent studies (HOUBRICK, 1989) on the anatomy of the extant *Campanile symbolicum* indicate that members of Campanilidae should no longer be considered as cerithioidean gastropods. He argued for a new systematic placement of *Campanile* at the base of, but outside, the cerithioidean clade. In addition, he suggested elevating the family Campanilidae to superfamilial status (as superfamily Campaniloidea Douvillé, 1904). PONDER & WARÉN (1988) and HOUBRICK (1989) rejected HASZPRUNAR's (1988) idea that *Campanile* is in any way related to heterobranch gastropods.

Campanile greenellum Hanna & Hertlein, 1939

(Figures 3–5)

Campanile greenellum HANNA & HERTLEIN, 1939:101–102, fig. 1; KEEN & BENTSON, 1944:137.

Original description: “Shell elongate conic, imperfect but with about 8 whorls. The top of each whorl ornamented by a band of elevated nodes, there being about 22 on the last whorl; below each band of nodes there are three revolving cords separated from each other and from the nodose band above and below by incised lines. Length (incomplete) approximately 95 mm, greatest width 64 mm” (HANNA & HERTLEIN, 1939:101).

Type material and type locality: Holotype CAS 7233, near Devils Slide along California State Highway 1, south of San Francisco, San Mateo County, northern California.

Geographic distribution: Santa Monica Mountains, Los Angeles County, southern California (herein) to Stewarts Point, Sonoma County, northern California.

Stratigraphic distribution: “Martinez Stage” (upper Paleocene): Santa Susana Formation, Santa Monica Mountains, southern California (herein, LACMIP locs. 24433 and 27023); lower San Francisquito Formation, Redrock Mountain, southern California (herein, LACMIP loc. 24716); unnamed strata near Devils Slide along California State Highway 1, south of San Francisco, northern California (HANNA & HERTLEIN, 1939); German Rancho formation (informal), northern California (WENTWORTH, 1966, 1968).

Remarks: The mudstone and siltstone rocks at the type locality of *Campanile greenellum* near Devils Slide are unnamed and have been referred to (MORGAN, 1981) as Paleocene turbidites.

WENTWORTH (1966, 1968) reported a specimen of *Campanile greenellum* from the Paleocene part of the informal German Rancho formation, west of the San Andreas fault, 2 km south of the town of Stewarts Point, northern California. The specimen, which was identified by W. O. Addicott, was found near the base of a sea cliff at Wentworth's field loc. 730 in a bed of pebble conglomerate with a matrix of very poorly sorted clayey sandstone (WENTWORTH, 1966:181). My attempts to find this specimen were unsuccessful. Macrofossils, which are sparse in the German Rancho formation, underwent post-mortem transport by means of turbidity currents into a deep-water environment, and the rocks containing the *Campanile* specimen have undergone right slip of at least 435 km (270 miles) along the San Andreas fault (WENTWORTH, 1968). The German Rancho formation *Campanile* specimen, therefore, originally lived in the vicinity of the southeastern Diablo Range or the Temblor Range, south-central California. The northern limit of the original distribution of *C. greenellum* along the Pacific coast of North America during the Paleocene, therefore, was approximately the same as that for the Eocene-age *C. dilloni*.

SEIDERS & JOYCE (1984:table 1) found a specimen of ?*Campaniliopa* [sic] n. sp. from an unnamed mudstone unit at LACMIP loc. 27203 in the northern Santa Lucia Range, central California coastal area. The specimen was associated with a few other mollusks and some brachiopods. The *Campanile* specimen and its associated fauna are stored at LACMIP. SEIDERS & JOYCE (1984) assigned a tentative late Paleocene age to the fossils. I examined the *Campanile* specimen from loc. 27203 and found it to be a deeply weathered fragment of an internal mold that shows only a small part of the body whorl. The specimen can be identified only as *Campanile* sp. indet.

Campanile dilloni (Hanna & Hertlein, 1949)

(Figures 6–11)

Campanilopa dilloni HANNA & HERTLEIN, 1949:393, pl. 77, figs. 2, 4, text-fig. 1; GIVENS, 1974:69, pl. 7, fig. 10; SQUIRES & ADVOCATE, 1986:853, 855, fig. 2.1.

Campanile dilloni Hanna & Hertlein: SQUIRES, 1991b:pl. 1, fig. 18.

Original description: “Shell elongate, 4 whorls present (shell incomplete on type); whorls rather flat-sided but slightly concave; top of each whorl sculptured with a projecting carina which bears about 14 to 16 pointed nodes, the sides of the whorls are ornamented by about a half dozen spiral lirae. Paratypes in longitudinal section reveal the presence internally of two strong plaits on the columella and a rounded ridge on both the top and bottom of the cavity. Dimensions of holotype: height (incomplete), 72.5 mm; diameter, 44.0 mm. Some specimens, poorly preserved, indicate a height of approximately 300 mm” (HANNA & HERTLEIN, 1949:393).

SQUIRES & ADVOCATE (1986:853) gave a supplementary description: “Turreted-elongate shell of very large size;

protoconch and upper spire missing; whorls slightly concave, becoming flat sided in later whorls; posterior portion of each whorl with a very projecting, greatly thickened carina with eight to ten pointed nodes, sides of whorls with three to four swollen spiral cords; groove along inside of carina in later whorls; outer lip missing and aperture obscured by matrix."

Type material and type locality: Holotype CAS 9425 and paratypes CAS 9428 and 9429, all from CAS loc. 30667; Mabury Formation, Agua Media Creek, Temblor Range, Kern County, south-central California.

Geographic distribution: Orocopia Mountains, Riverside County, southern California, to Agua Media Creek, Temblor Range, Kern County, south-central California.

Stratigraphic distribution: California "Meganos Stage" (uppermost Paleocene to lower lower Eocene) to "Capay Stage" (middle lower Eocene). "MEGANOS STAGE": Uppermost Santa Susana Formation, Bus Canyon, south side of Simi Valley, Ventura County, southern California (herein, CSUN loc. 1565). "CAPAY STAGE": Lower Maniobra Formation, Orocopia Mountains, Riverside County, southern California (SQUIRES & ADVOCATE, 1986; SQUIRES, 1991b); lower Llajas Formation, Bus Canyon, south side of Simi Valley, Ventura County, southern California (herein, CSUN loc. 703); lower Juncal Formation, Sespe Hot Springs, Ventura County, southern California (GIVENS, 1974); Mabury Formation, Agua Media Creek, Temblor Range, Kern County, south-central California (HANNA & HERTLEIN, 1949). LOWER EOCENE (no differentiation as to stage): Sierra Blanca Limestone, near Oso Canyon, Santa Ynez River Valley, Santa Barbara County, southern California (herein, CSUN loc. 1566); Sierra Blanca Limestone, Lazaro Canyon, near Lake Cachuma, Santa Barbara County, southern California (NELSON, 1925; herein, CSUN loc. 955 = UCMP loc. A-2990).

Remarks: HANNA & HERTLEIN (1949) reported that the type locality (CAS loc. 30667) of *Campanile dilloni* extended along the outcrop for a distance of approximately 0.8 km. In 1992, I visited the type locality and found outcrops to be only moderately well exposed and consisting of a relatively thin section of conglomeratic sandstone that grades upward into very fine sandstone. I found macrofossils only in one small area that is equivalent to the middle of their reported band of outcrop. Very sparse macrofossil fragments of colonial corals and a few naticid gastropods were found in the basal sandstone. These fragmentary fossils have undergone considerable post-mortem transport. No new specimens of *C. dilloni* were found. Overlying and underlying the sandstone are thick sequences of mudstones. MALLORY (1970) interpreted the mudstones as bathyal deposits and the intervening sandstone (his middle member of the Lodo Formation) as a littoral deposit. ALMGREN *et al.* (1988) referred to the intervening sandstone as the Mabury Formation, and on the basis of

calcareous nannofossil biostratigraphy, assigned an age that is equivalent to the "Capay Stage."

NELSON (1925:348) reported numerous casts of *Campanile* sp., some of which, if unbroken, would be over 40 cm in length, from white limestone near Lake Cachuma, along Cachuma Creek, Santa Barbara County, southern California. He did not mention a specific locality, nor did he mention whether or not any specimens were stored at UCMP (the institution he was affiliated with). While going through the UCMP collections, I came across several large, poorly preserved casts of *Campanile* from UCMP loc. A-2990 (Cachuma Creek area). According to locality records at UCMP, this locality is the same as UCMP loc. 4124. KEENAN (1932:79, fig. 1) noted that UCMP loc. 4124 is the same as LSJU locality 1106 (in the Sierra Blanca Limestone). The specimens from UCMP loc. A-2990 = LSJU 1106, therefore, must be the ones that NELSON (1925) reported. Unfortunately, the exact location of this locality is not available in the register of localities at UCMP. The description given in these records mentions only nearness to Cachuma Creek. The description given by KEENAN (1932:79) mentions the "east fork of Cachuma Creek" but also mentions a longitude and latitude that are equivalent to the Pacific Ocean off the coast of Baja California. On an index map in KEENAN (1932:fig. 1), however, LSJU loc. 1106 is shown to be on a prominent east fork of Cachuma Creek.

I visited the area of UCMP loc. A-2990 and found four large, poorly preserved internal molds of *Campanile* at CSUN loc. 955 along the west side of Lazaro Creek, which is a prominent east fork of Cachuma Creek. Locality 955, which must be the same as UCMP loc. A-2990, coincides with the easternmost exposure of a thin band of Sierra Blanca Limestone on DIBBLEE's (1966:pl. 3) geologic map of the area. On this map, the thin band of outcrop is labelled "Tsb" for the Sierra Blanca Limestone, but the graphic pattern on the map corresponds to the Pliocene Careaga Sandstone. The specimens at CSUN loc. 955 have the diagnostic narrow pleural angle and large shell size of *C. dilloni*, and they are virtually identical to the specimen (Figure 8) of *C. dilloni* from the lower Llajas Formation and the specimen (Figures 9, 10) of *C. dilloni* from the Sierra Blanca Limestone near Oso Canyon. Because the campanilid from CSUN loc. 955 has never been illustrated before, the best preserved specimen is shown in Figure 11.

Campanile n. sp.? SQUIRES (1987:31-32, figs. 32, 33) from the lower Juncal Formation ("Capay Stage") in the Whitaker Peak area, Los Angeles County, southern California, may be *C. dilloni* but poor preservation prevents a positive identification.

SQUIRES & DEMETRION (1992:28, fig. 65) reported a specimen of *Campanile* sp. from the lower Eocene ("Capay Stage") part of the Bateque Formation, Baja California Sur, Mexico, but the specimen is so poorly preserved that no species identification is possible. SQUIRES (1992) reported *Campanile* sp. from the "Capay Stage" part of the

Tepetate Formation, Baja California Sur, Mexico, but poor preservation prevents species identification.

ACKNOWLEDGMENTS

Antony J. Marro (CSUN) collected and donated the specimen of *Campanile dilloni* from the upper Santa Susana Formation. Fen Yan (CSUN) collected and donated the specimen of *C. dilloni* from the Sierra Blanca Limestone in Oso Canyon. Michael P. Gring (CSUN) obtained permission for access to private property (type section of *C. dilloni*). Michael P. Gring and Martin Jackson (CSUN) and Lindsey T. Groves (Natural History Museum of Los Angeles County, Malacology Section) helped in field work. Carl Twisselman (Buttonwillow, California) kindly allowed access to private property (type section of *C. dilloni*). Carl M. Wentworth (U.S. Geological Survey, Menlo Park) provided locality information, and he and Chuck Powell, Jr., (U.S. Geological Survey, Menlo Park) tried to find the specimen of *Campanile greenellum* from the German Rancho formation. Louella Saul (LACMIP) allowed access to collections, provided casts of the primary type material of *C. greenellum* and *C. dilloni*, and shared her knowledge about new Paleocene occurrences of *Campanile* in California. She and an anonymous reviewer critically read the manuscript.

LOCALITIES CITED

- CAS loc. 30667. "SW corner of sect. 27, T28S, R19E, through the NE $\frac{1}{4}$ of the SE $\frac{1}{4}$ of section 28, T28S, R19E, south side of headwaters of Media Agua Creek, Kern County, California" (HANNA & HERTLEIN, 1949: 393). A visit by the author resulted in the following refinement of this description: at elevation 2650 ft. (800 m) on a lowly resistant ridge formed by conglomeratic sandstone along the crest of the north side of Media Agua Creek, 442 m (1450 ft.) N and 183 m (600 ft.) E of SW corner of section 27, T28S, R19E, U.S. Geological Survey, 7.5-minute, Las Yeguas Ranch Quadrangle, 1959, Temblor Range, Kern County, south-central California. Mabury Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: Earl Dillon and R. L. Hewitt, 1940s?.
- CSUN loc. 703. At elevation of 1430 ft. (420 m) along a ridge on east side of Bus Canyon, S side of Simi Valley, 238 m (780 ft.) S and 177 m (580 ft.) W of NE corner of section 28, T2N, R18W, U.S. Geological Survey, 7.5-minute, Thousand Oaks Quadrangle, 1950 (photorevised 1967), Ventura County, southern California. Lower Lajas Formation, lowermost part of shallow-marine (transgressive) facies of SQUIRES (1984). Age: Middle early Eocene ("Capay Stage"). Collector: R. L. Squires, October 1988.
- CSUN loc. 955. At elevation of 2160 ft. (650 m), just below top of resistant hill formed by a 20-m-thick gray algal limestone along the west side of Lazaro Canyon, 533 m (1750 ft.) S and 91 m (300 ft.) W of the SE corner of section 23, T7N, R29W, U.S. Geological Survey, 7.5-minute, Figueroa Mtn. Quadrangle, 1959, Santa Barbara County, southern California. Sierra Blanca Limestone. Age: Early Eocene. Collectors: R. L. Squires and L. T. Groves, October 1985. Same as UCMP loc. A-2990, see below.
- CSUN loc. 1565. At elevation of 1100 ft. (340 m), along west side of Bus Canyon, S side of Simi Valley, on north bank of an unnamed tributary that enters Bus Canyon from the W, 274 m (900 ft.) S and 503 m (1650 ft.) W of NE corner of section 28, T2N, R18W, U.S. Geological Survey, 7.5-minute, Thousand Oaks Quadrangle, 1950 (photorevised 1967), Ventura County, southern California. Uppermost Santa Susana Formation. Age: Latest Paleocene or early early Eocene ("Meganos Stage"). Collector: A. J. Marro, 1985.
- CSUN loc. 1566. At elevation of 1919 ft. (600 m), approximately 1.15 km E of Oso Canyon, on hillside on north side of Santa Ynez River, 175 m (575 ft.) E and 191 m (625 ft.) S of NW corner of section 6, T5N, R27W, U.S. Geological Survey, 7.5-minute, San Marcos Pass Quadrangle, 7.5 minute, 1959 (photorevised 1988), Santa Barbara County, southern California. Sierra Blanca Limestone. Age: Early Eocene. Collector: F. Yan, 1986.
- LACMIP 24433. 150 m (500 ft.) NE of the end of the entry road to quarry in Trailer Canyon, stratigraphically just below white algal limestone, U.S. Geological Survey, 7.5-minute, Topanga Quadrangle, 1952 (photorevised 1967), Santa Monica Mountains, Los Angeles County, southern California. Santa Susana Formation. Age: Late Paleocene ("Martinez Stage"). Collector: J. Champeny, June 1961. Same as UCLA loc. 4433.
- LACMIP 24716. Approximately 3160 ft. (1000 m) elevation, on dip slope of Redrock Mountain, about 415 m (1400 ft.) S17 W of hill 3991, sec. 1, T6N, R17W, U.S. Geological Survey, 7.5-minute, Liebre Mountain Quadrangle, 1958 (photorevised 1974), NW San Gabriel Mountains, Los Angeles County, California. San Francisquito Formation. Age: Late Paleocene ("Martinez Stage"). Collector: E. C. Jests, August 1963. Same as UCLA loc. 4716.
- LACMIP 27023. Above drop off at about 1275 ft. (400 m) elevation, 100 m (325 ft.) NE of quarry symbol in Trailer Canyon, below white algal limestone, U.S. Geological Survey, 7.5-minute, Topanga Quadrangle, 1952 (photorevised 1967), Santa Monica Mountains, Los Angeles County, southern California. Santa Susana Formation. Age: Late Paleocene ("Martinez Stage"). Collectors: L. R. Saul and J. Alderson, June 1982. Same as UCLA loc. 7023.
- LACMIP 27203. West-flowing tributary to Arroyo Seco, approximately 160 m W of the Indians Road, approximately 3.5 km N and 0.5 km E of the SW corner of U.S. Geological Survey, 7.5-minute, Junipero Serra Peak

- Quadrangle, 1949, northern Santa Lucia Range, Monterey County, California. Unnamed mudstone. Age: Tentatively, late Paleocene ("Martinez Stage"). Collector: V. M. Seiders, 1982. Same as loc. 1 of SEIDERS & JOYCE (1984:fig. 3).
- LSJU 1106. "Santa Ynez Quad.; west bank of the East Fork of Cachuma Creek, just north of right-angled bend in stream, R28W, T6N, 3½ miles west and ¾ mile south (to scale of U.S.G.S. topographic map) of intersection of Long. 119°49'W and Lat. 34°40'N" (KEENAN, 1932: 79), Sierra Blanca Limestone, Santa Barbara County, southern California. Same as UCMP loc. A-2990 (see below) = UCMP loc. 4124 = CSUN loc. 955.
- UCMP A-2990. "Limestone near Cachuma Canyon." Sierra Blanca Limestone. Age: Early Eocene. Collector: R. N. Nelson, early 1920s. Same as UCMP loc. 4124 = LSJU loc. 1106 = CSUN loc. 955.
- UCMP 4124. Same as UCMP loc. A-2990, see above.
- WENTWORTH field loc. 730. "Near base of the sea cliff in a 3-m-thick bed of pebble conglomerate with a matrix of very poorly sorted clayey sandstone. The bed lies near the top of a section of sandstone and conglomerate which is overlain by mudstone and fine-grained sandstone" (WENTWORTH, 1966:181); 1.35 km N and 1.4 km W of SE corner of U.S. Geological Survey, 7.5-minute, Stewarts Point Quadrangle, 1978, Sonoma County, northern California. German Rancho formation (informal). Age: Late? Paleocene. Collector: C. M. Wentworth, circa 1963.
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ADDENDUM

Recent collecting by William P. Elder (U.S. Geological Survey, Menlo Park) near Stewarts Point in northern California has yielded several specimens of *Campanile greenellum* from the Paleocene part of the German Rancho formation in the same area that WENTWORTH (1966, 1968) reported this species. Elder plans to include a discussion and figures of these specimens as part of a paper on the molluscan paleontology of the Cretaceous and Paleocene rocks in this area.

Larval Morphology of the Scallop *Argopecten purpuratus* as Revealed by Scanning Electron Microscopy

by

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Abstract. Larval development of the scallop *Argopecten purpuratus* (Lamarck, 1819) is described from trochophore stage to metamorphosis using scanning electron microscopy. The trochophore developed by about 12 hr post fertilization (20–22°C), the early D-stage veliger developed by about 24–36 hr post fertilization, and the larval stage is about 16–20 days in duration. The ready to metamorphose veliger larvae have a mean length of 231 μm . The larval hinge (provinculum) has a constant length during the larval life and no ligament is seen before metamorphosis. The development of *A. purpuratus* follows in general that described for other pectinids. Some differences in larval morphology from that of other pectinids (*i.e.*, ornamentation of prodissococonch I and hinge morphology) are discussed.

INTRODUCTION

Pectinid larvae are gaining considerable attention due to the economic importance of scallops and the availability of larvae in laboratory and hatchery cultures. Although numerous studies have investigated various aspects of larval pectinid development (DIX & SJARDIN, 1975; DIX, 1976; DiSALVO *et al.*, 1984; ROSE & DIX, 1984; PAULET *et al.*, 1988; HODGSON & BOURNE, 1988; ROSE *et al.*, 1988) few have described embryonic and larval morphology in detail. SASTRY (1965) characterized the morphology of larval and post-larval stages of *Argopecten irradians concentricus* (Say, 1822) and HODGSON & BURKE (1988) described in detail the embryonic and larval morphology of *Chlamys hastata* (Sowerby, 1843). Some studies have provided ultrastructural details of larval organs in *Pecten maximus* (Linnaeus, 1758): the morphogenesis of the larval valves (LE PENNEC, 1974), the ultrastructure of the statocysts (CRAGG & NOTT, 1977), the glands of the larval foot (GRUFFYDD *et al.*, 1975), the major components of the musculature (CRAGG, 1985), and the ciliated rim of the velum (CRAGG, 1989). In order to identify bivalve larvae within the plankton, or characterize larval developmental stages, hinge morphology in several pectinids has been described (LE PENNEC, 1974, 1980; DIX, 1976; LUTZ *et al.*, 1982, 1985; URIBE *et al.*, 1982; ROSE & DIX, 1984; TREMBLAY *et al.*, 1987; ROSE *et al.*, 1988). Recently CRAGG & CRISP (1991) have published a comprehensive review

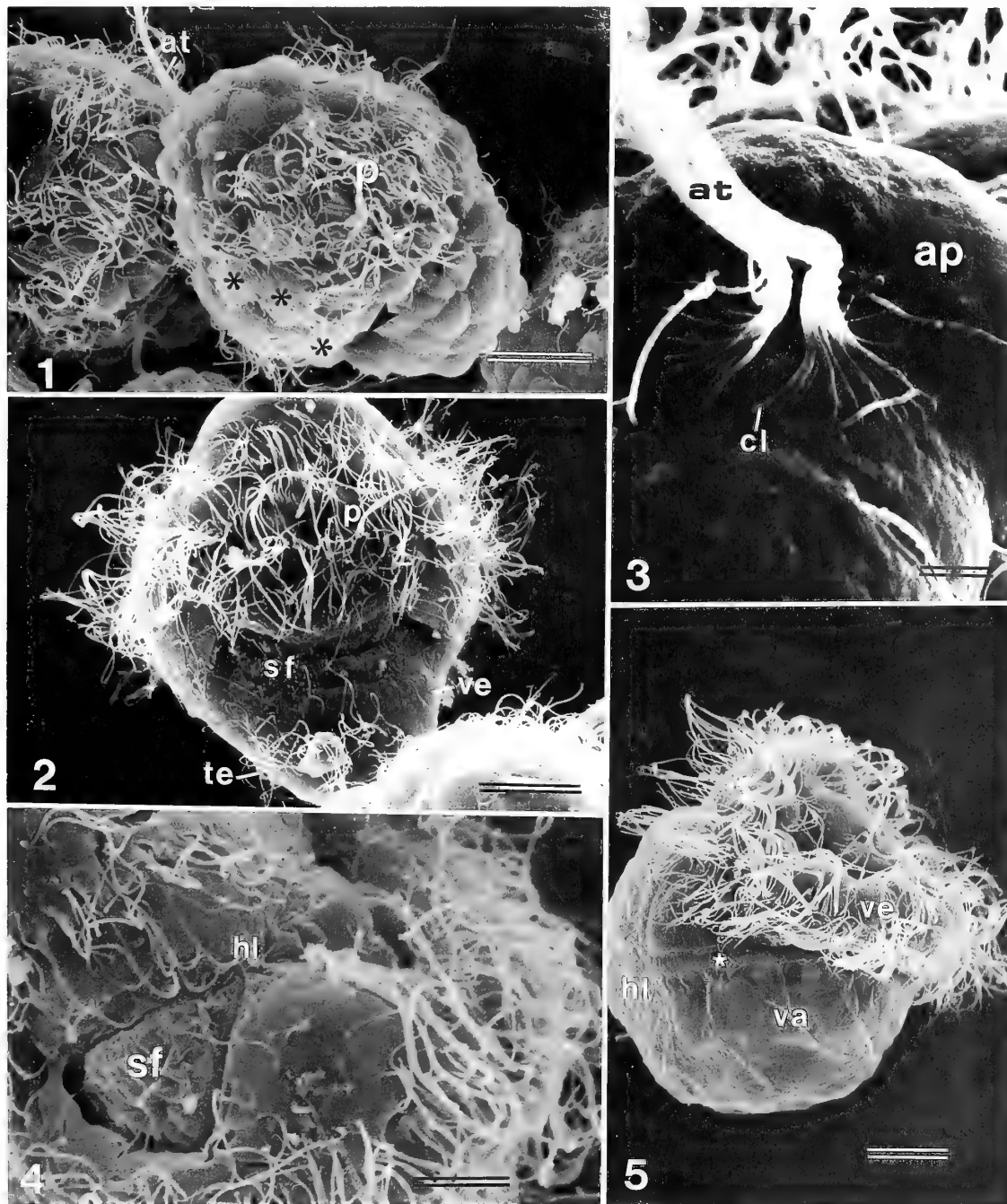
of the biology of scallop larvae that includes morphology, physiology, behavior, distribution, and rearing methodology, among others.

The scallop *Argopecten purpuratus* is a functional hermaphrodite inhabiting the northern coast of Chile and the southern coast of Perú. Although it is massively produced, few studies have been carried out on this species and they have been mainly concerned with mass culture (DiSALVO *et al.*, 1984), population dynamics (WOLFF, 1987, 1988), chromosome number (VON BRAND *et al.*, 1990), and biochemical composition (MARTÍNEZ, 1991). The objective of this study is to describe the morphology of *A. purpuratus* from the trochophore stage up to metamorphosis, providing detailed descriptions of the trochophore, valves, velum, muscles, digestive system, foot, and gills.

MATERIALS AND METHODS

Trochophore, veliger, and pediveliger larvae were obtained from the hatchery facilities at the Universidad Católica del Norte, Coquimbo, Chile, where this species is cultured according to the method of DiSALVO *et al.* (1984) at a temperature of 20–22°C.

Specimens were relaxed using 1:1 15% solution of MgCl_2 and seawater at room temperature (16–18°C) for 1–5 min, and fixed in 2% glutaraldehyde in 0.025 M cacodylate-buffered seawater at pH 8.3 (TURNER & BOYLE, 1975). The specimens were dehydrated in a graded series of eth-



Explanation of Figures 1 to 5

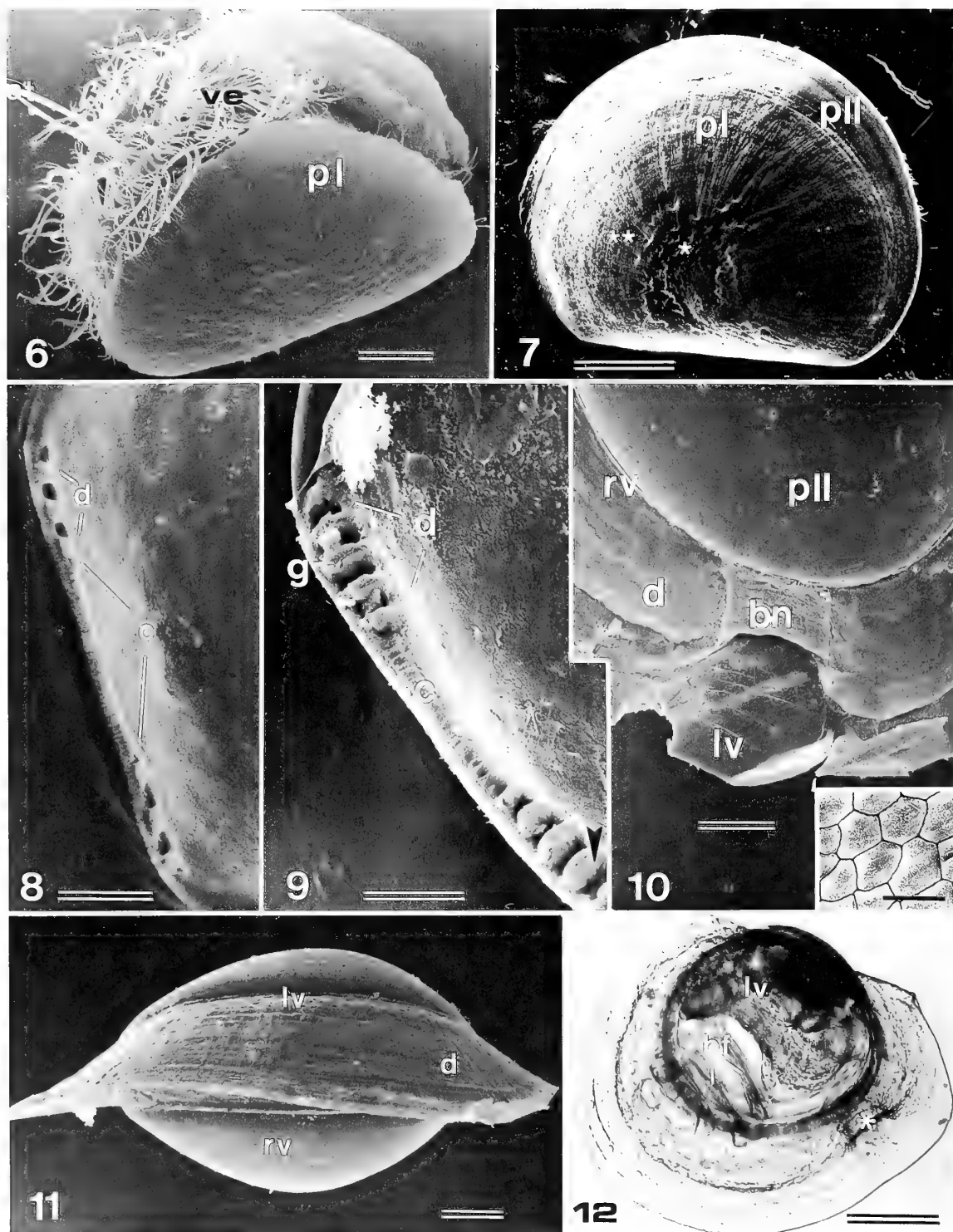
Figure 1. Early trochophore larva with partially removed vitelline envelope; prototroch (p) and primary trochoblasts (*); invagination of the shell field (arrowhead); apical tuft (at). SEM. Scale bar = 10 μ m.

Figure 2. Late trochophore larva with evaginating shell field (sf); telotroch (te); prototroch (p), vitelline envelope (ve). SEM. Scale bar = 10 μ m.

Figure 3. Anterolateral view of trochophore; apical plate (ap) with apical tuft (at); cilium (cl). SEM. Scale bar = 2 μ m.

Figure 4. Dorsal view of late trochophore larva with developing shell field (sf); hinge line (hl). SEM. Scale bar = 5 μ m.

Figure 5. Early D-stage larva; valve (va); thickened border (*); developing velum (ve); hinge line (hl). SEM. Scale bar = 10 μ m.



Explanation of Figures 6 to 12

Figure 6. Early D-stage larva with calcified valves; prodissoconch I (pI); velum (ve); apical tuft (at). Note punctate-stellate ornamentation on external surface of valve. SEM. Scale bar = 10 μ m.

Figure 7. External view of right valve of D-stage larva; prodissoconch I (pI); prodissoconch II (pII); punctate region (*); stellate region (**). SEM. Scale bar = 20 μ m.

anol, critical point dried using CO₂ as a transitional fluid, and mounted on double scotch tape (DST). The valves of some larvae were removed by slightly pressing and lifting a wooden pick wrapped in DST. Samples were gold coated and examined on a JEOL JSM T300. Whole mounts were made by adding Orange G stain to the 95% ethanol solution during the dehydration process and mounting in Entellan Mounting Medium (Merck).

In order to remove the vitelline envelope, some trochophore larvae were treated with 1 mM EDTA in calcium-free seawater for 5 min before fixation.

Shell dimensions, measured by light microscopy, were length (anteroposterior distance parallel to hinge), height (dorsoventral distance from hinge line or umbo to ventral margin of shell), and provinculum length (distance between outside denticles along the hinge line) for 30 specimens at each larval stage.

RESULTS

Trochophore

The trochophore stage is attained after 8–12 hr post-fertilization (pf) at a temperature of 20–22°C and has a mean length of 70 μ m. The gastrula does not hatch from its vitelline envelope; the latter is maintained through the trochophore stage, being shed gradually until the formation of the D-stage veliger. The trochophore is typically pyriform with a well-developed 15–20- μ m broad prototroch of simple cilia that surrounds the broader part of the larva; these cilia develop from three to four rows of primary trochoblasts (Figure 1). The prototroch cilia are the first to develop, while the telotroch is visible only in the late trochophore stage; the latter is formed by a narrow band of simple cilia that surround the base of the larva (Figure 2). The apical tuft is situated in the center of the apical plate and is formed by a group of 28–32 clustered cilia 15–20 μ m long (Figure 3). The invagination of the shell gland occurs very early, at the gastrula stage; it is located on the dorsal surface of the trochophore and is visible as a transverse crack (Figure 2). The mouth opening is located opposite to the shell gland on the ventral surface and, due to the presence of the vitelline envelope, is hardly visible as a round pit.

Veliger and Pediveliger Larvae

Valves: The evagination of the shell gland takes place at a late trochophore stage, and the shell field consists of two

equal, oval areas of periostracum that are divided by a straight mark that corresponds to the hinge line (Figure 4). The oval shell field is surrounded by a thicker border (Figure 5) that probably corresponds to the limit of the shell gland; it disappears once the valves are calcified. The time of calcification was not observed, but by 20 hr pf most larvae had calcified valves. The prodissoconch I has a central round area, about 20 μ m in diameter, with pits and radial striations. This configuration has been termed a "punctate-stellate pattern" (CARRIKER & PALMER, 1979) (Figure 6). By 24–36 hr pf, the prodissoconch I has grown and both valves are able to contact each other while enclosing completely the soft body of the larva. At this point commarginal growth lines appear in the prodissoconch, which is now known as prodissoconch II (Figure 7). In this stage the valves have three symmetrical denticles at each side of the hinge line and a slightly striated cardinal region is visible (Figure 8). The mean hinge line length is 69 μ m and the valves measure 107 μ m in length and 83.3 μ m in height. The provinculum or larval hinge of the 8-day-old larva presents five symmetrical denticles on either side; each denticle presents a groove along its crown and some transverse ridges on the sides; the cardinal region is striated (Figure 9), and the mean hinge line length is 95 μ m. The provinculum is maintained through the rest of the larval life; there is no increase in its length or in the number of denticles, and the valves are symmetrical up to metamorphosis. When pediveligers reach a mean shell length of 231 ± 10 μ m they are fully competent to metamorphose. The dissoconch or adult shell appears once the pediveliger has settled (16 to 20 days pf) and metamorphosis is completed. The texture of the dissoconch is clearly different from that of the prodissoconch; both valves are more flexible and break easily with manipulation. The secretion of the adult left valve is initiated first and is marked by a pitted appearance and weak radial and concentric striations while the right valve presents a prismatic ornamentation (Figures 10, 11). The byssal notch is formed in the latter during metamorphosis (Figures 10, 12). The ligament and the ligament pit were observed only in metamorphic larvae.

Digestive system: At 48 hr pf, the "D" larva has a developed digestive system, which is not basically different from the adult stage. At 8 days pf it consists of a mouth located under the velum at the posterior side, a foregut, a stomach, a digestive gland, an intestine, and an anus that is located dorsal to the mouth (Figure 13). The mouth is

Figure 8. Provinculum of 2-day-old larva; denticles (d); striated cardinal region (c). SEM. Scale bar = 10 μ m.

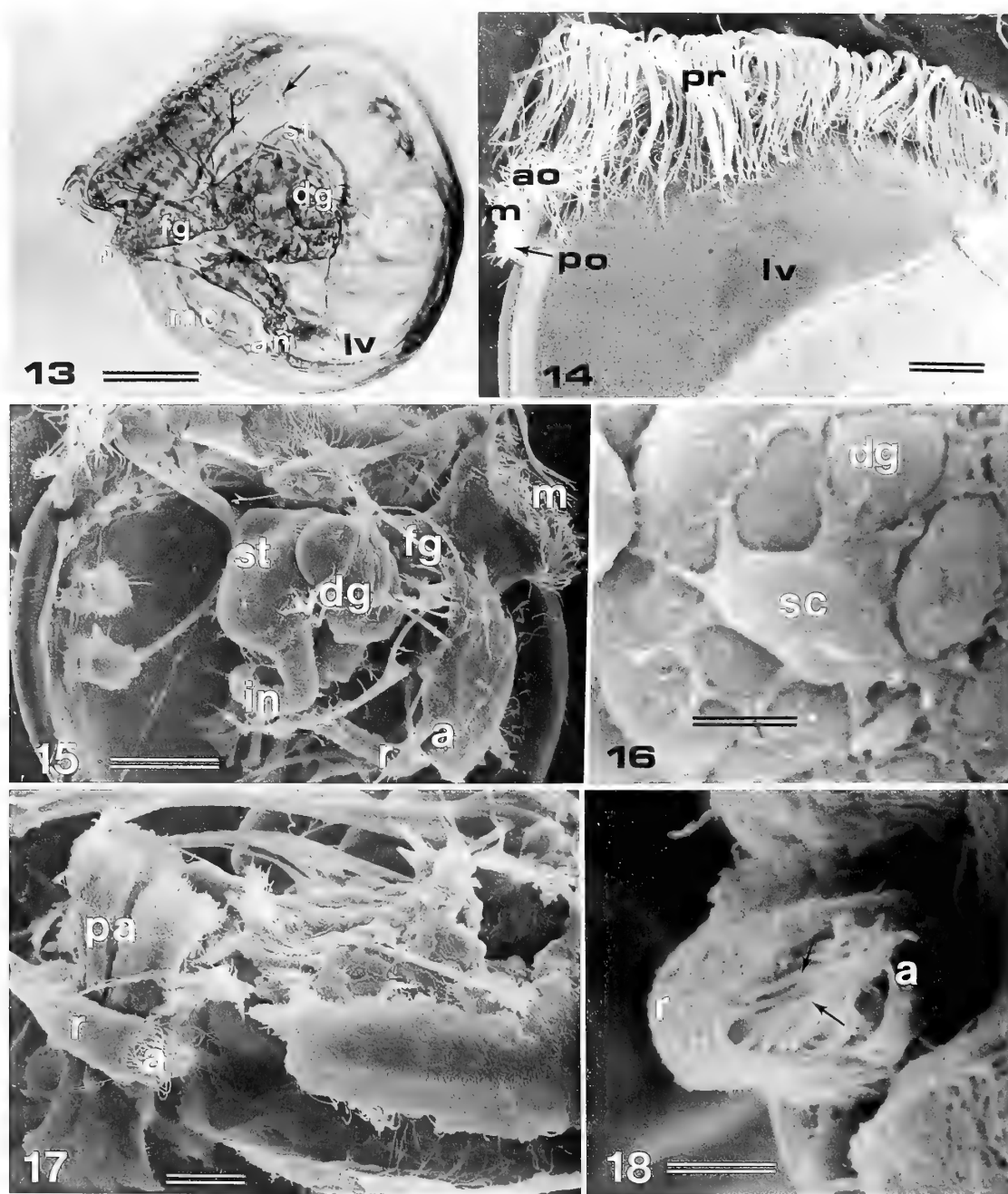
Figure 9. Provinculum of 8-day-old larva; denticles (d); striated cardinal region (c); longitudinal groove (g); transverse grooves (arrowhead). SEM. Scale bar = 10 μ m.

Figure 10. Partial external view of metamorphic larva; right valve (rv); dissoconch (d); byssal notch (bn); prodissoconch II (pII);

left valve (lv). SEM. Scale bar = 20 μ m. Insert: detail of prismatic structure of right valve. SEM. Scale bar = 5 μ m.

Figure 11. Anterior view of whole metamorphic larva; left valve (lv); right valve (rv); dissoconch (d). SEM. Scale bar = 25 μ m.

Figure 12. Lateral view of left valve (lv) of metamorphic larva; byssal notch (*) viewed through the left valve; branchial filaments (bf). LM. Scale bar = 50 μ m.



Explanation of Figures 13 to 18

Figure 13. Lateral view of left valve (lv) of 8-day-old veliger larva; foregut (fg); mouth (m); stomach (st); digestive gland (dg); intestine (in); anus (a); mantle cavity (mc); velar retractor muscles (arrows). LM. Scale bar = 25 μ m.

Figure 14. Lateral view of anterior region of 8-day-old larva; mouth (m); postoral cilia (po); adoral cilia (ao); preoral cilia (pr); left valve (lv). SEM. Scale bar = 10 μ m.

Figure 15. Internal view of a late veliger stage larva; mouth (m); foregut (fg); stomach (st); digestive gland (dg); intestine (in); rectum (r); anus (a). SEM. Scale bar = 20 μ m.

Figure 16. Detail of digestive gland surface of an early pediveliger larva; stellate cell (sc); digestive gland (dg). SEM. Scale bar = 2 μ m.

Figure 17. Internal view of a late veliger stage larva; rectum (r); anus (a); posterior adductor muscles (pa). SEM. Scale bar = 10 μ m.

Figure 18. Detail of Figure 17. Opening of the anus (a) with cilia (arrows); rectum (r). SEM. Scale bar = 2 μ m.

surrounded dorsally by postoral cilia and ventrally by adoral cilia (Figure 14). A postanal tuft of a few simple cilia is placed dorsal to the anus. The mantle cavity is evident at this stage of development.

On the late veliger-pediveliger stage, the foregut is funnel shaped and continues into the stomach, which has a smooth surface (Figure 15). The digestive gland surrounds each side of the stomach and presents on its surface a netlike array of prolongations from a few stellate cells (Figure 16) that probably correspond to a nerve net. The intestine coils once and the rectum passes dorsal to the posterior adductor muscle (Figure 17). The opening of the anus is located in the mantle cavity, dorsal to the larval mouth, and cilia project from its lumen (Figure 18).

Muscles: In 6–8-day-old veligers, the velar retractor muscles run obliquely in an anterior-posterior direction. They branch at their insertion in each valve; the same is observed at their insertion in the velum (Figures 13, 19, 20), and the branching continues as the larva grows. A maximum of four pairs of velar retractors was observed.

Early veliger larvae have two anterior adductor muscles (Figure 20) and are the only adductors present in this stage. The posterior adductor muscle is formed at a late veliger stage (11-day-old) by a series of muscle bundles (Figure 21) that develop into the posterior adductor muscle. The anterior adductors are not observed after metamorphosis.

Velum: The larval velum is located at the posteroventral end of the larva (Figure 22). It is oval shaped, surrounded by cilia, and represents the locomotory and feeding organ of the larva. The apical tuft disappears at early prodissoconch II stage. The most pronounced ciliary band corresponds to the preoral band formed by long compound cilia (Figure 23). When deciliation is induced by excess of $MgCl_2$, the preoral band is seen to be derived from two to three rows of cells, each bearing five to six compound cilia and each one formed by the clustering of about 12 simple cilia (Figure 24). External to the preoral band there is an adoral band of simple cilia that are shorter than the preoral ones except for those on the ventral side of the mouth, which are longer (Figure 23). A postoral band is situated around the dorsal side of the mouth. Some simple cilia are present inner to the preoral band, but they are not organized as a well-defined band. During metamorphosis the velum can be shed completely as one unit or can be deciliated gradually before being histolyzed. The cilia continue beating on their own for up to 10–15 min, and they are probably shed with their basal structures (Figure 25).

Foot and gills: At 9–10 day pf a foot primordium is observed in the mantle cavity between the mouth and the anus. A ciliated heel and a nonciliated toe rudiment are distinguished. The byssal duct is observed in the toe-heel junction. At this time the gill rudiments emerge from the

mantle at either side of the foot (Figures 26, 27). At 15 days pf, the foot is well developed and the toe has lengthened; all the ventral surface of the toe and heel is densely covered with simple cilia. The lateral surface of the foot is nonciliated. The foot is fully functional and larvae are seen either crawling on the substrate or swimming. A ciliated duct is observed at the base of either side of the foot (Figures 29, 30). The gills have developed in five pairs of ciliated filaments located at each side in the mantle (Figure 12).

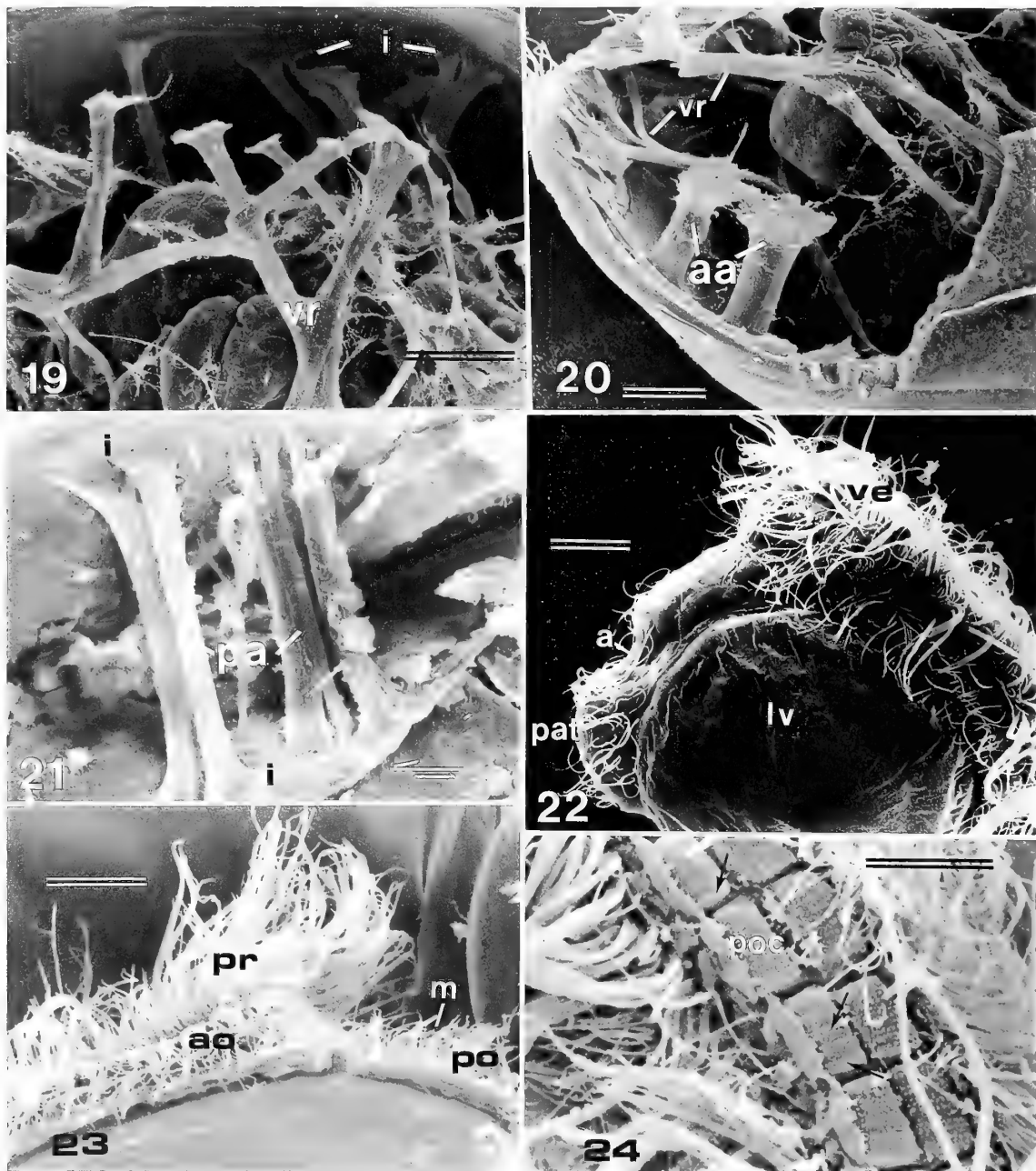
The inner mantle fold shows two kinds of grouping of cilia: type “a” that consists of a group of up to ten cilia of 1.7 to 1.8 μm length emerging from a protuberance, and type “b” that consists of a single cilium of 1.0 to 2.1 μm length projecting from a circular depression. Both are alternately distributed along the mantle fold (Figures 27, 28).

DISCUSSION

The development of *Argopecten purpuratus* follows in general that described for other pectinids (SASTRY, 1965; HODGSON & BURKE, 1988; CRAGG & CRISP, 1991). Although several authors have reported the time of development of some stages of pectinid larvae (Table I), interspecific comparisons become difficult because experimental temperatures, as well as rearing conditions, are not uniform. Nevertheless, it may be noted that the trochophore and early D-stage larvae of *A. purpuratus* are attained in a shorter time than for *A. irradians concentricus* reared at a higher temperature ($24 \pm 1^\circ C$), whereas metamorphosis is reached within the same time for both species. The mean lengths at metamorphosis for all species in Table 1 are within a similar range of 200–250 μm with the exception of *Amusium balloti* (Bernardi, 1861), which metamorphoses over a wide range of lengths, from 172 to 374 μm . The size of metamorphic larvae of *A. purpuratus* is well within the range described for other pectinids (CRAGG & CRISP, 1991).

The maintenance of the vitelline envelope in the trochophore stage and its gradual shedding during larval development have not been reported before. In a similar study of *Chlamys hastata* (HODGSON & BURKE, 1988) the vitelline envelope was shed in the gastrula stage, when the larva hatches; other studies of pectinids do not refer to this process.

The punctate-stellate pattern on the prodissoconch I of *Argopecten purpuratus* is similar to that described for other pectinids (LUCAS & LE PENNEC, 1976; HODGSON & BURKE, 1988) and for other bivalve larvae (ANSELL, 1961, 1962; CARRIKER & PALMER, 1979; WALLER, 1981). However, in *A. purpuratus* the pattern is circular and covers an area of about 20 μm in diameter, about half the size of the region of *Chlamys hastata* that is oval shaped. The pattern in *A. purpuratus* also differs from that described for other species (CARRIKER & PALMER, 1979; WALLER, 1981), sug-



Explanation of Figures 19 to 24

Figure 19. Internal view of 8-day-old veliger larva; branched velar retractor muscles (vr); insertion on internal surface of valve (i). SEM. Scale bar = 10 μ m.

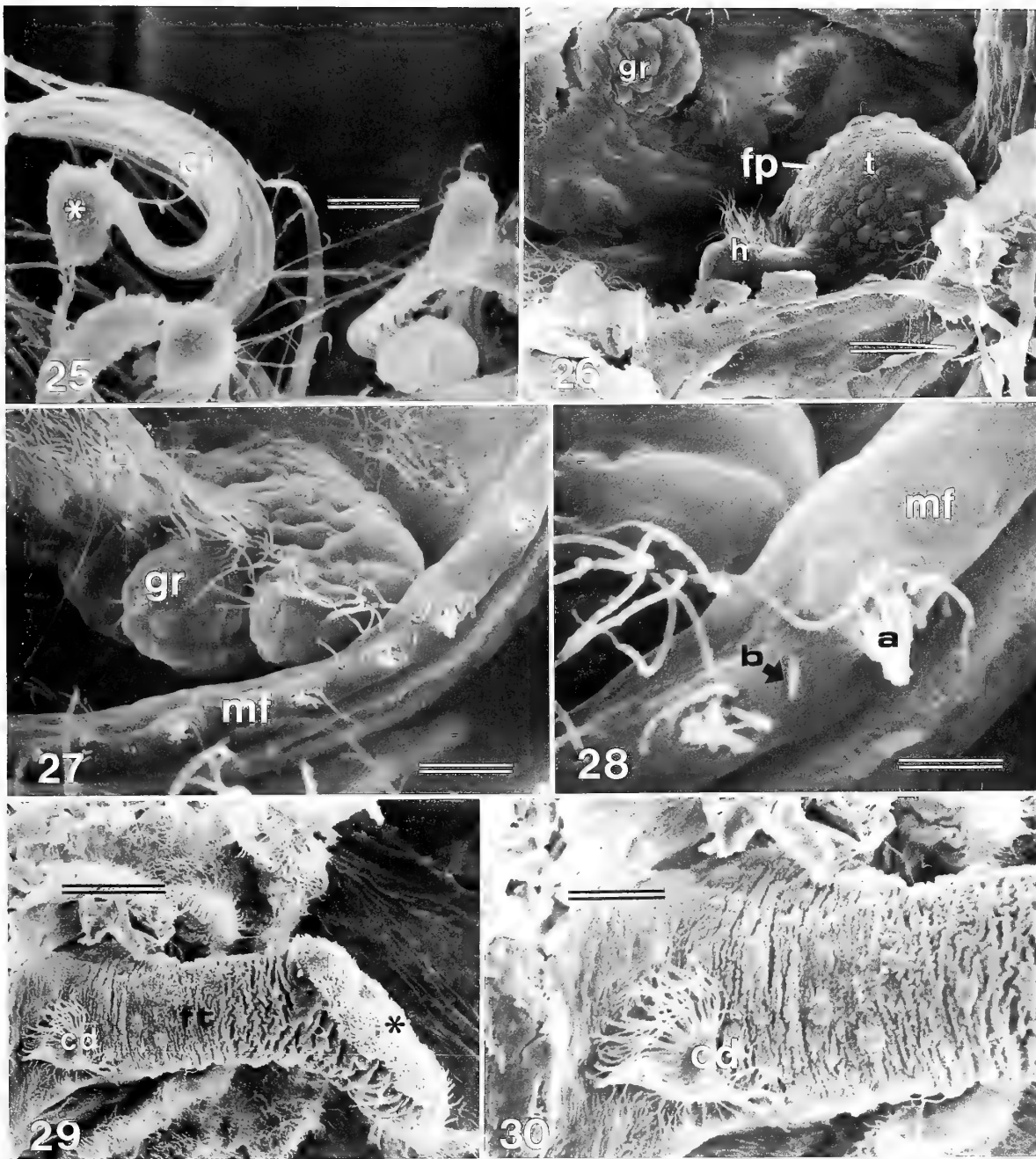
Figure 20. Internal view of 8-day-old veliger larva; anterior adductor muscles (aa). Velar retractor muscles (vr). SEM. Scale bar = 10 μ m.

Figure 21. Internal view of 11-day-old veliger larva showing developing posterior adductor muscle (pa); insertion on internal surface of valves (i). SEM. Scale bar = 10 μ m.

Figure 22. External view of transition trochophore to D-stage larva, about 18 hr pf; left valve (lv); velum (ve); postanal tuft (pat); anus (a). SEM. Scale bar = 10 μ m.

Figure 23. Mouth region of 8-day-old veliger larva; preoral band (pr); adoral band (ao); postoral band (po); mouth (m). SEM. Scale bar = 10 μ m.

Figure 24. Detail of deciliated preoral band cells (poc) of 12-day-old veliger larva, showing cilia "scars" rows (arrows). SEM. Scale bar = 5 μ m.



Explanation of Figures 25 to 30

Figure 25. Cilia (ci) shed from velum during settlement; basal structure (*). SEM. Scale bar = 5 μ m.

Figure 26. Internal view of mantle cavity of early pediveliger larva; foot primordium (fp); heel (h); toe rudiment (t); gill rudiments (gr). SEM. Scale bar = 10 μ m.

Figure 27. Internal view of mantle cavity of 10-day-old veliger larva; gill rudiment (gr); mantle fold (mf). SEM. Scale bar = 5 μ m.

Figure 28. Detail of Figure 27; mantle fold (mf); ciliary grouping type "a" (a); ciliary grouping type "b" (b). SEM. Scale bar = 2 μ m.

Figure 29. Mantle cavity of 15-day-old pediveliger larva; foot (ft); toe (t); heel (h); ciliated ventral surface (*); ciliated duct (cd). SEM. Scale bar = 20 μ m.

Figure 30. Detail of Figure 29; ciliated duct (cd). SEM. Scale bar = 10 μ m.

Table 1

Time of development of some stages of pectinid larvae under laboratory conditions. pf = post-fertilization.

	Temp. °C	Trochophore		Early D		Metamorphosis	
		Hours pf	Mean length (μ m)	Hours pf	Mean length (μ m)	Days pf	Mean length (μ m)
<i>Argopecten purpuratus</i> (present study)	20–22	8–12	70	24–36	107	16–20	231 \pm 10
<i>Chlamys hastata</i> (HODGSON & BURKE, 1988)	14–16	30	60	50	105	40	240
<i>Argopecten irradians</i> <i>concentricus</i> (SASTRY, 1965)	23–25	24	—	48	101	15–19	190–200
<i>Chlamys (Chlamys)</i> <i>asperimus</i> (ROSE <i>et al.</i> , 1984)	17–18	24	70	48	108	20	170–250
<i>Pecten maximus</i> (GRUFFYDD, 1972)	16	20	—	40–50	—	33–38	250
<i>Amusium balloti</i> (ROSE <i>et al.</i> , 1988)	18–19	28	85.5	48	123	22–27	172–374

gesting this character might be of taxonomic importance and a possible tool for identification of early planktonic stages.

The prodissoconch II ornamentation (commarginally striate) does not differ from that of other pectinids (MERRILL, 1961; LUTZ *et al.*, 1982; URIBE *et al.*, 1982; HODGSON & BURKE, 1988; CRAGG, 1989) and the initiation of it occurs about the same time, when the prodissoconch I is able to enclose the soft body of the larva. This supports the suggestion of WALLER (1981) that the prodissoconch II is secreted by the rim of the mantle and the prodissoconch I is secreted by the shell gland.

The basic hinge morphology of *Argopecten purpuratus* is similar to that of other pectinids—hinge teeth at each end with a thin, slightly striated cardinal ridge that lacks teeth. Nevertheless, there is variability in the total number of teeth as well as the number on the anterior and posterior hinge side. They vary from a total of seven teeth for *Chlamys asperima* (Lamarck, 1819) (ROSE & DIX, 1974) with three and four hinge teeth at each end, to 10 or 12 symmetrically placed on *C. hastata* (HODGSON & BURKE, 1988) (Table 1). In *A. purpuratus* the number of teeth increases during larval development, although the provinculum length remains constant throughout larval life, indicating that teeth are added to the inside; this was described for the first time in *Chlamys hastata* (HODGSON & BURKE, 1988). Also, as described for the latter species, *A. purpuratus* presents on each denticle a longitudinal groove and transverse ridges on the sides.

The dissoconch of *Argopecten purpuratus* is similar in shape and ornamentation to *Placopecten magellanicus* (Gmelin, 1791) (MERRILL, 1961) and to *Chlamys hastata*

(HODGSON & BURKE, 1988) and to the general description of other pectinid dissoconchs (CRAGG & CRISP, 1991). In *A. purpuratus* the ligament pit seems to be characteristic of metamorphic larvae, so it is possible that the ligament appears in larvae that are in the process of metamorphosis. A ligament pit was not observed in ready to metamorphose larvae as described for *Chlamys hastata* (HODGSON & BURKE, 1988).

The arrangement and number of velar retractors and the branching of the retractors that increases as the larva grows is similar to *Pecten maximus* (CRAGG, 1985). Also, the anterior adductor muscle that is formed by two columns and the posterior adductor that is formed by several muscle bundles not organized in columns corresponds to those described for *P. maximus*. We did not do further histological analysis to determine which part of each adductor corresponds to striate or to smooth muscle, as this was not possible to do by means of SEM.

In *Argopecten irradians concentricus* (SASTRY, 1965) the sensory tentacles appear on post-larvae as small papillary projections on the mantle margin; the eyes appear later as pink protuberances on the mantle alternating with the tentacles. In *A. purpuratus* the protuberances with clusters of cilia may be interpreted as developing tentacles. The ciliary duct observed on the foot probably conforms to the statocyst duct as in *Pecten maximus* (CRAGG & NOTT, 1977) and in *Ostrea edulis* (WALLER, 1981).

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A Review of *Pitar* (*Hyphantosoma*) Dall, 1902 (Veneridae: Pitarinae) and a Description of *Pitar* (*H.*) *festoui* sp. nov.

by

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Abstract. *Hyphantosoma* Dall, 1902, a tropical subgenus of *Pitar* (Bivalvia: Veneridae), is characterized by fine zigzag sculpture. It includes six fossil species: four from the Caribbean, one from the eastern Pacific, and one from New Zealand. Of the five living species, three occur in the eastern Pacific. A fourth species, *P. (H.) intricata* (Dautzenberg, 1907), occurs in the west Pacific. A fifth species, *P. (H.) festoui* sp. nov., is herein described from Tahiti, French Polynesia.

INTRODUCTION

Unlike other major subfamilies in the Veneridae Rafinesque, 1815, no recent published revision exists of the Pitarinae Stewart, 1930, and it remains one of the least understood venerid subfamilies. The nominate genus *Pitar* Römer, 1857, contains 50 or more extant species; KEEN (1969) lists 11 extant subgenera, including *Hyphantosoma* Dall, 1902. *Hyphantosoma* includes pitarine clams with fine zigzag sculpture on their valves, a rare sculptural pattern within the family. Here I review the species of this taxon, describe their past and present distribution, discuss their relationships with other pitarine taxa, and describe a new species.

Museum abbreviations: Academy of Natural Sciences at Philadelphia, ANSP; National Science Museum at Tokyo, NSMT; United States National Museum, USNM; University of California Museum of Paleontology, UCMP.

SYSTEMATIC ACCOUNT

Genus *Pitar* Römer, 1857

Subgenus *Hyphantosoma* Dall, 1902

Hyphantosoma DALL, 1902:354; type species (original designation): *Cytherea (Circe) carbasea* Guppy, 1866.

Definition: Valves have fine, chiseled zigzag sculpture on part or all of the surface; ovate to subovate and subtrigonal profiles; large lunules; well-developed anterior lateral teeth; smooth internal margins.

Description: DALL (1902) described the taxon simply as

“shell with zigzag sculpture on the surface like *Textivenus* Cossmann, of the Venerine series,” and the sculpture itself as “fine zigzag chiseling of the surface.” Zigzag sculpture is often restricted to the sides; it is evident over the entire surface of *Hyphantosoma aletes* Hertlein & Strong, 1948, but small specimens lack the sculpture, and it is easily eroded off larger specimens (HERTLEIN & STRONG, 1948). Zigzag sculpture is more sharply defined in the tropical mid- and western Pacific species.

Extant species of *Hyphantosoma* have ovate valves, typically with slightly to more pronounced subquadrate posterior ends. The escutcheon is often well defined by a slight ridge, an uncommon state within Pitarinae. The lunule is large, moderately obese, and distinctly, if shallowly, incised. The cardinal teeth are typical of Pitarinae: the right anterior and posterior teeth are dorsally attached, as are the left anterior and median teeth, and the right anterior tooth is partially detached from the hinge plate. The left anterior lateral tooth is well developed, compact, and either close to or moderately separate from the cardinal teeth. The sculpture is of fine, polished, indistinct growth bands, superimposed partly or entirely by fine, nested, zigzag threads. The pallial sinus is well developed, moderately deep, and triangular, with a rounded apex. The valves are white, porcelaneous, often patterned with brown marks or rays, and range from 2 to 8 cm in length.

Remarks: DALL (1902) observed that among American taxa the surface zigzag sculpture is present in Oligocene species, becoming obsolete in the Pliocene and is present only within the shell matrix for Recent species, becoming evident in worn specimens, with color patterns that fre-

quently follow the zigzag pattern. In fact, zigzag sculpture, although not sharply highlighted, occurs on the surface of all three Recent American species. Traces of zigzag sculpture occur on the posterior surface of the type of *Hyphantosoma pollicaris* (Carpenter, 1864) (USNM 1372), and of *H. hertleini* Olsson, 1961 (OLSSON, 1961; herein, Figure 2c).

Distribution: The taxon is recorded in fossils ranging from the Early Oligocene to early Pleistocene in the Caribbean (WOODRING, 1982). Several fossil species are recorded from this area and one species from New Zealand. The biogeographic range of living species is exclusively subtropical and tropical Pacific. In the west Pacific, specimens of *Hyphantosoma* have been recorded from the Philippines (HABE & OKUTANI, 1983), southern Japan (HABE, 1981; MATSUKUMA, 1984), Truk and Ponape of the Eastern Caroline Islands (MATSUKUMA, 1984), and Tahiti in the south Pacific (HARTE, 1992). I have personally collected beachdrift specimens from Java, Indonesia, near Jakarta. In the eastern Pacific, *Hyphantosoma* occurs from the Gulf of California to Peru (KEEN, 1971). All species are uncommon to rare, and occur in subtidal offshore sediments of mud, gravelly or shelly sand (HERTLEIN & STRONG, 1948), or coralline sand (HARTE, 1992).

Fossil Species

Pitar (Hyphantosoma) carbacea (Guppy, 1866)

(Figure 1a–d)

Cytherea (Circe) carbacea GUPPY, 1866:292, pl. 18, fig. 13; PALMER, 1927:56, pl. 10, figs. 1, 4, 13, 14.

Description: Length, 36 mm; height, 30 mm; semidiameter, 15 mm. A thin, ovate shell sculptured with close, fine, distinct radial grooves that curve upward laterally and broadly zigzag medially (WOODRING, 1925).

Remarks: GUPPY (1866) noted that the sculpture is similar to that of *Gafrarium divaricatum* (Gmelin, 1791), although the latter's sculpture consists of the threads describing a few large zigzags, and not the many small zigzags characteristic of *Hyphantosoma*.

Type material: Holotype, British Museum, Natural History 64086.

Distribution: Miocene. Bowden, Jamaica; Santo Domingo.

Pitar (Hyphantosoma) semipunctata (Conrad, 1848)

(Figure 1e, f)

Cytherea semipunctata CONRAD, 1848:134, pl. 13, fig. 19; PALMER, 1927:55, pl. 10, figs. 5, 9.

Description: Length, 14 mm; height, 12 mm; semidiameter, 4 mm. An ovate shell sculptured with close, narrow but distinct commarginal ribs, crossed by a zigzag series of punctations.

Remarks: CONRAD (1848) presents no written description of the species, and both his figure and those of PALMER (1927) do not show the zigzag series of punctations, indicating that this sculpture is weak and is dominated by the commarginal ribs.

Type material: Holotype, ANSP 30658.

Distribution: Oligocene. Vicksburg, Mississippi (type location).

Pitar (Hyphantosoma) floridana Dall, 1903

(Figure 1g)

DALL, 1903:1267, pl. 54, fig. 10; PALMER, 1927:56, pl. 10, fig. 6.

Description: Length, 29 mm; height, 24 mm; width, 17 mm. A solid, subtrigonal shell sculptured with fine commarginal threads, crossed by close, fine, faint zigzag sculpture that appears obsolete anteriorly but present elsewhere. Posterior end emphasized by one or two slight radial ridges; lunule long, rather narrow.

Type material: Holotype, USNM 114753.

Distribution: Lower Miocene. Chipola horizon at Alum, and on the Chipola River at McDonald's farm, Florida.

Pitar (Hyphantosoma) opisthogrammata Dall, 1903

(Figure 1l)

DALL, 1903:1267, pl. 54, fig. 8; PALMER, 1927:58, pl. 10, fig. 2.

Description: Length, 39 mm; height, 32 mm; width, 22 mm. A subovate, somewhat trigonal shell with a slightly subquadrate posterior end sculptured with fine commarginal lines; fine zigzag sculpture is mostly obsolete, usually discernible only ventrally. Lunule deeply impressed, sharply incised, with a second, fainter, lunular furrow paralleling the ventral boundary.

Remarks: Similar in shape to *Pitar floridana*, *P. opisthogrammata* has much less zigzag sculpture, no posterior ridge, and a distinctly different lunule.

Type material: Holotype, USNM 109232.

Distribution: Pliocene. Marl of Shell Creek and Alligator Creek near Charlotte Harbor, Florida.

A single fossil species is recorded from Panama:

Pitar (Hyphantosoma) centangulata
Brown & Pilsbry, 1911

(Figure 1h–k)

BROWN & PILSBRY, 1911:369; PALMER, 1927:264–265, pl. 10, figs. 7, 8, 10, 12; WOODRING, 1982:686–687, pl. 122, figs. 4–8, 11.

Description: Length, 51 mm; height, 40 mm; semidiameter, 16 mm. A thin ovate shell without any posterior ridge;

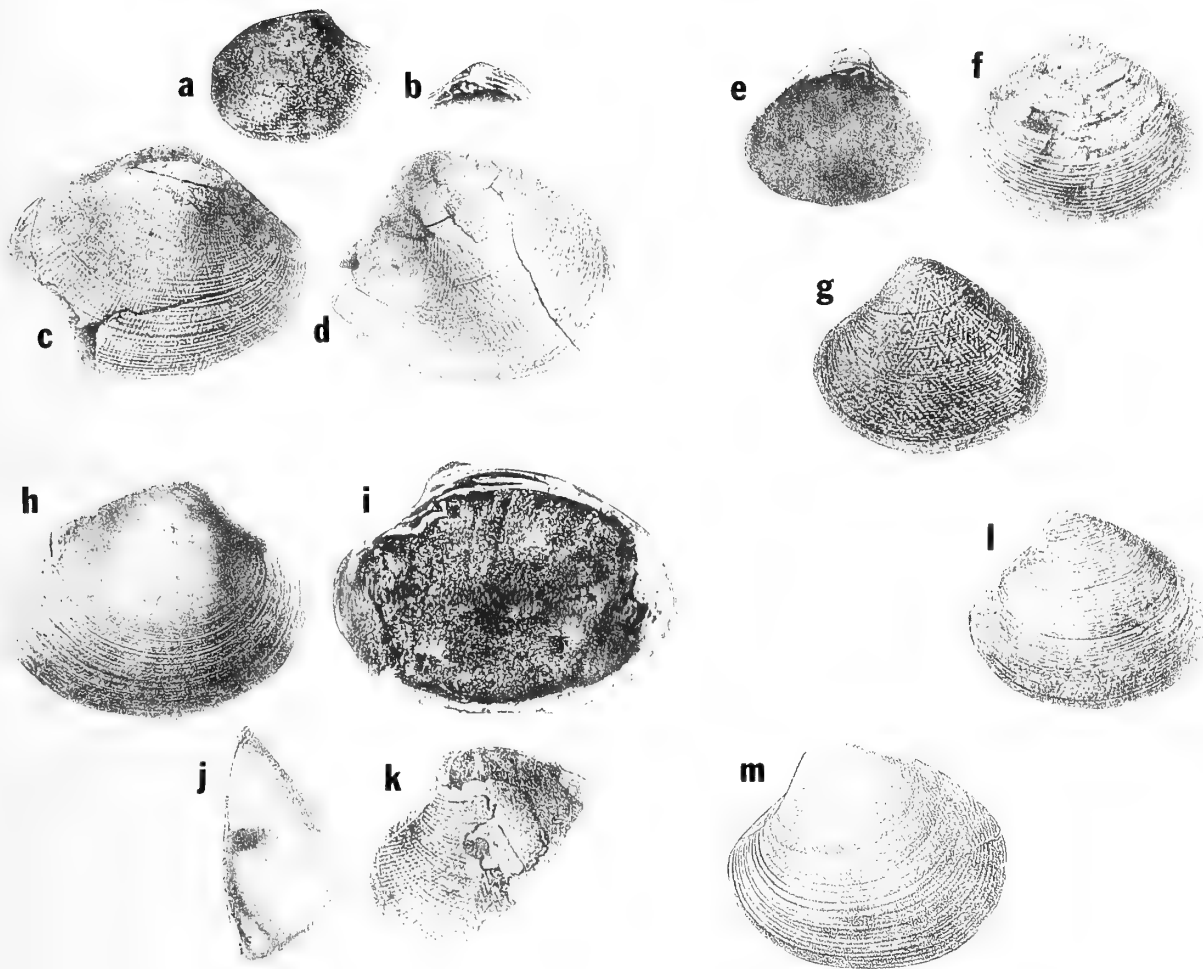


Figure 1

a-d. *Pitar (Hyphantosoma) carbasea* (Guppy). a. Length (L) = 36 mm. b. Hinge of right valve. c. L = 37 mm. d. L = 44 mm. e, f. *P. (Hyphantosoma) semipunctata* (Conrad). e. L = 11.5 mm. f. L = 14 mm. g. *P. (Hyphantosoma) floridana* Dall, L = 30 mm. h-k. *P. (Hyphantosoma) centangulata* Brown & Pilsbry. h, i. L = 52 mm. j. L = 36 mm, semidiameter = 13 mm. l. *P. (Hyphantosoma) opisthogrammata* Dall, L = 32 mm (1a-l from PALMER, 1927). m. *P. (Hyphantosoma) sculpturata* (Marshall), L = 30 mm (from BEU & MAXWELL, 1990).

fine zigzag sculpture is obsolete dorsally but otherwise present.

Remarks: The sculpture of *Pitar centangulata* is similar to that of *P. floridana*, although the former is larger, differently shaped, and lacks a posterior ridge. Observing no real differences in shape and areas with zigzag sculpture between *P. centangulatus* and *P. carbasea*, WOODRING (1982) distinguished them solely on the zigzag sculpture which, PALMER (1927) observed, was much finer in *P. centangulatus*.

Type material: Holotype, ANSP 1764.

Distribution: Early-Mid Miocene. Gatun Locks excavations of Canal Zone, Panama: Quarry on west side of Gatun locks.

MARWICK (1927) noted one fossil species from New Zealand:

Pitar (Hyphantosoma) sculpturata (Marshall, 1918)

(Figure 1m)

Macrocallista sculpturata MARSHALL, 1918:272, pl. 20, figs. 6-6a; MARWICK, 1927:594-595, pl. 41, figs. 74-76.

Description: Length, 30 mm; height, 20 mm; width, 25 mm. A broadly ovate to subovate shell sculptured with fine commarginal lines superimposed by faint fine zigzag sculpture, strongest at both ends; it is very thin (A. Beu, personal communication). The left anterior lateral is long, well separated from the cardinals, and the lunule is large.

Remarks: BEU & MAXWELL (1990) note that the Clifden

specimens differ from the Pakaurangian topotypes in having narrower but higher umbones and might not be conspecific with them.

Type material: Holotype, TM 4567, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand.

Distribution: Upper Oligocene: Otaian-Altonian. New Zealand: Pakau-rangi Point, Kaipara (type location); bed 6A, Clifden, Southland; east of the Puketoi Range, southern Hawke's Bay.

Key to Fossil Species of *Hyphantosoma*

1. Pacific species 2
1. Atlantic species 3
2. New Zealand species; ovate; sculpture of many fine zigzags *sculpturata*
2. Eastern Pacific species; ovate; zigzag sculpture of curving radials laterally and broad zigzag medially *centangulata*
3. Zigzag sculpture consists of series of punctations crisscrossing distinct commarginal cords *semipunctata*
3. Zigzag sculpture consists of fine, close-set threads and grooves 4
4. Shell ovate, thin; zigzag sculpture of curving radials laterally, broad zigzag centrally *carbacea*
4. Shell subovate to subtrigonal; zigzag sculpture of several zigzags 5
5. Subtrigonal; posterior end with 1 or 2 slight radial ridges; zigzag sculpture absent anteriorly *floridana*
5. Subovate, somewhat subtrigonal; posterior end slightly subquadrate, with no radial ridges; zigzag sculpture usually only discernible ventrally *opisthogrammata*

Living Species

Of the five living species, three occur in the eastern Pacific:

Pitar (Hyphantosoma) aletes Hertlein & Strong, 1948

(Figure 3F)

HERTLEIN & STRONG, 1948:172–173, pl. 1, figs. 9, 11–13; OLSSON, 1961:277–278, pl. 49, fig. 3; KEEN, 1971:170, fig. 404.

Description: Length, 54 mm; height, 46 mm; width, 34 mm. A white, subovate, somewhat subtrigonal shell sculptured with fine, polished commarginal lines, superimposed by fine close zigzag sculpture covering most of the shell. Zigzag sculpture is absent on juveniles and possibly some specimens (HERTLEIN & STRONG, 1948). The pallial sinus is less than half the shell length.

Remarks: HERTLEIN & STRONG (1948) noted that *Pitar aletes* closely resembles *P. carbacea* but has a more angular

posterior end. OLSSON (1961) stated that it closely resembles *P. pollicaris* (Carpenter, 1864), below, but *P. aletes* is deeper (height vs. length), more trigonal and more convex.

Type material: Holotype, California Academy of Sciences, CAS 065554.

Distribution: Gulf of California to Costa Rica. Depth 77–110 m. Rare.

Pitar (Hyphantosoma) hertleini Olsson, 1961

(Figure 2c, d)

OLSSON, 1961:276–277, pl. 45, figs. 6–6a; KEEN, 1971:170, fig. 405.

Description: Length, 36 mm; height, 29 mm; width, 19.5 mm. An ovate shell sculptured with fine polished commarginal lines, with traces of zigzag sculpture evident on its posterior end, but otherwise obscure or absent. It is richly patterned with brown zigzag markings and radial rays against a cream white background.

Remarks: OLSSON (1961) notes it is thinner, smaller, more strongly colored and with more convex valves than *Pitar pollicaris*, below. The patterns and coloring resemble some *P. (Pitar) newcombianus* (Gabb, 1865) from Baja California, Mexico, and California, but *P. hertleini* has a broader posterior end, blunter anterior end and zigzag sculpture.

Type material: Holotype, ANSP 218921.

Distribution: Panama to Peru. Rare.

Pitar (Hyphantosoma) pollicaris (Carpenter, 1864)

(Figure 2a)

Callista pollicaris CARPENTER, 1864:312; OLSSON, 1961:277, pl. 49, figs. 7–7a; KEEN, 1971:170, fig. 406.

Description: Length, 66 mm; height, 57 mm; width, 36 mm. A large, ovate, white shell, with zigzag sculpture present in adults as faint traces at the ends. Juveniles have zigzag markings and sculpture; pallial sinus long, extending to nearly half the shell length (KEEN, 1971). It is the largest species of *Hyphantosoma* (Figure 1a), a large specimen measuring: length, 80 mm, height, 60 mm, width, 39 mm (HERTLEIN & STRONG, 1948).

Remarks: HERTLEIN & STRONG (1948) note that the species resembles *Pitar (Pitar) prora* (Conrad, 1837) (see Figure 2b).

Type material: Holotype, USNM 13721.

Distribution: Gulf of California to Colombia. The species probably occurs just beyond the low tide line (KEEN, 1971); it has been dredged from sandy bottoms at 13–14 m. Rare.

Two more species exist in the tropical west and South Pacific, respectively:

Pitar (Hyphantosoma) intricata (Dautzenberg, 1907)

(Figure 3D, E)

Meretric (Pitar) intricata DAUTZENBERG, 1907:333–334, pl. 6, fig. 1. *Callogonia philippinensis* HABE & OKUTANI, 1983:1–3; figs. 1–4. *Pitar (Hyphantosoma) limatulum* (Sowerby, 1851), of HABE, 1977, and MATSUKUMA, 1984, non Sowerby, 1851.

Description: Length, 50 mm; height, 41 mm; width, 31 mm. This ovate shell is sculptured with fine, polished, indistinct, commarginal lines, superimposed by fine zigzag sculpture over most of the shell (Figure 3D, E). The umbones are prominent, and the posterior end is broad and rounded. The left anterior lateral tooth is compact and relatively close to the anterior cardinal, unlike in other living species. The shell is often patterned with flecked or solid brown rays of variable width, sometimes traversed by concentric bands of brown.

Type material: Holotype, Laboratoire de Biologie des Invertébrés Marins et Malacologie collection, Museum National d'Histoire Naturelle, Paris. Hypotypes, NSMT Mo-61187, NSMT Mo-54072.

Distribution: Kii Peninsula, Japan; the Philippines; Celebes; Java, Indonesia; Ponape and Truk, Eastern Caroline Islands. Depth: 10–42 m. Uncommon.

Pitar (Hyphantosoma) festoui Harte, sp. nov.

(Figure 3A–C)

Pitar (Hyphantosoma) sp.: HARTE, 1992:7, cover figs. 9–10.

Description: Length, 22 mm; height, 18 mm; width, 14 mm. An ovate shell sculptured with fine, polished, indistinct, commarginal lines, superimposed by fine zigzag sculpture over most of the shell (Figure 3A–C). It is marked irregularly with light brown patches of variable size, sometimes almost forming large, irregular, compounded chevrons. A bib of deep rosy red extends laterally on either side from the base of the umbo, skirting the border of the lunule, and fading anteriorly to the main part of the escutcheon. A gray concentric band, occurring medially, interrupts the otherwise white background of the type specimen. The escutcheon is fairly well defined, and marked with a few brown zigzags. The lunule is large, moderately obese, and distinctly incised. In the left valve, a compact, well-developed, anterior lateral tooth is moderately separated from the cardinal teeth. A moderately thick, triangular anterior cardinal is connected dorsally to a longer, wedge-shaped median cardinal. The posterior cardinal is a long, narrow ridge. In the right valve, there are two smaller anterior lateral teeth, and a short triangular anterior cardinal connected to and aligned perpendicularly to a long, narrow, slightly bifid posterior cardinal. The right median cardinal is short, triangular, close to and in

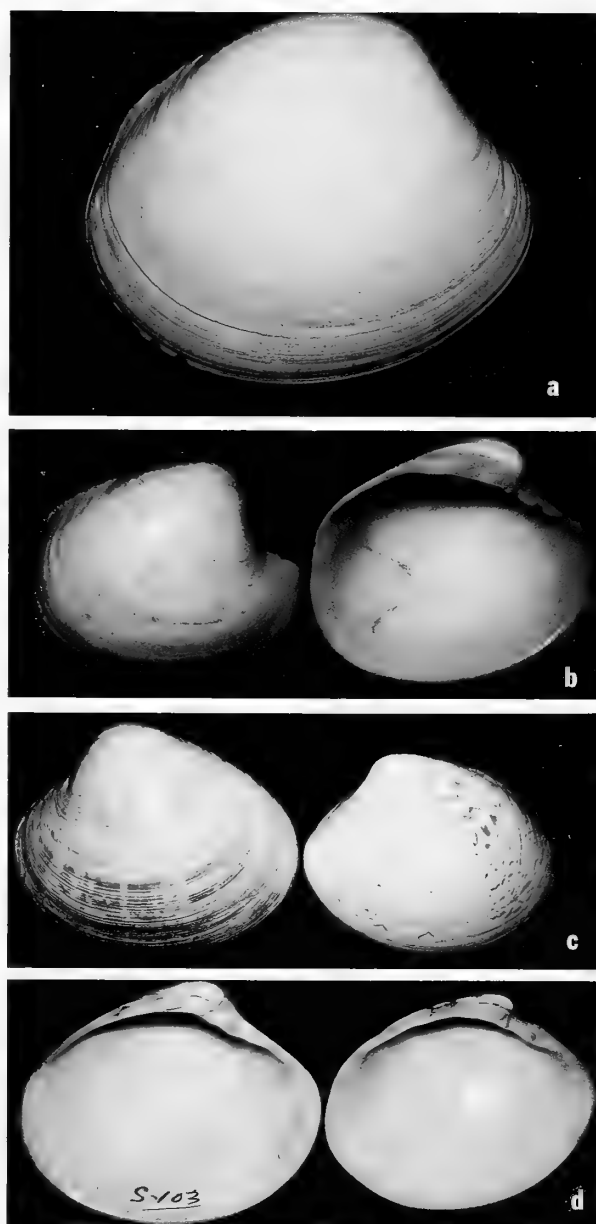


Figure 2

a. *Pitar (Hyphantosoma) pollicaris* (Carpenter), Baja California, Mexico, Length (L) = 64 mm. b. *Pitar (Pitar) prora* (Conrad), Tahiti, L = 34 mm. c, d. *Pitar fulminatus* (Menke), Florida, L = 50 mm (left), *P. (Hyphantosoma) hertleini* Olsson, Baja California, Mexico, L = 46 mm (right). c. Exteriors. d. Interiors. UCMP specimens.

parallel with the anterior cardinal. The pallial sinus is deep, triangular, and rounded at the apex.

Remarks: While the sculpture of *Pitar festoui* is similar to that of *P. intricata*, the anterior end of *P. festoui* is more

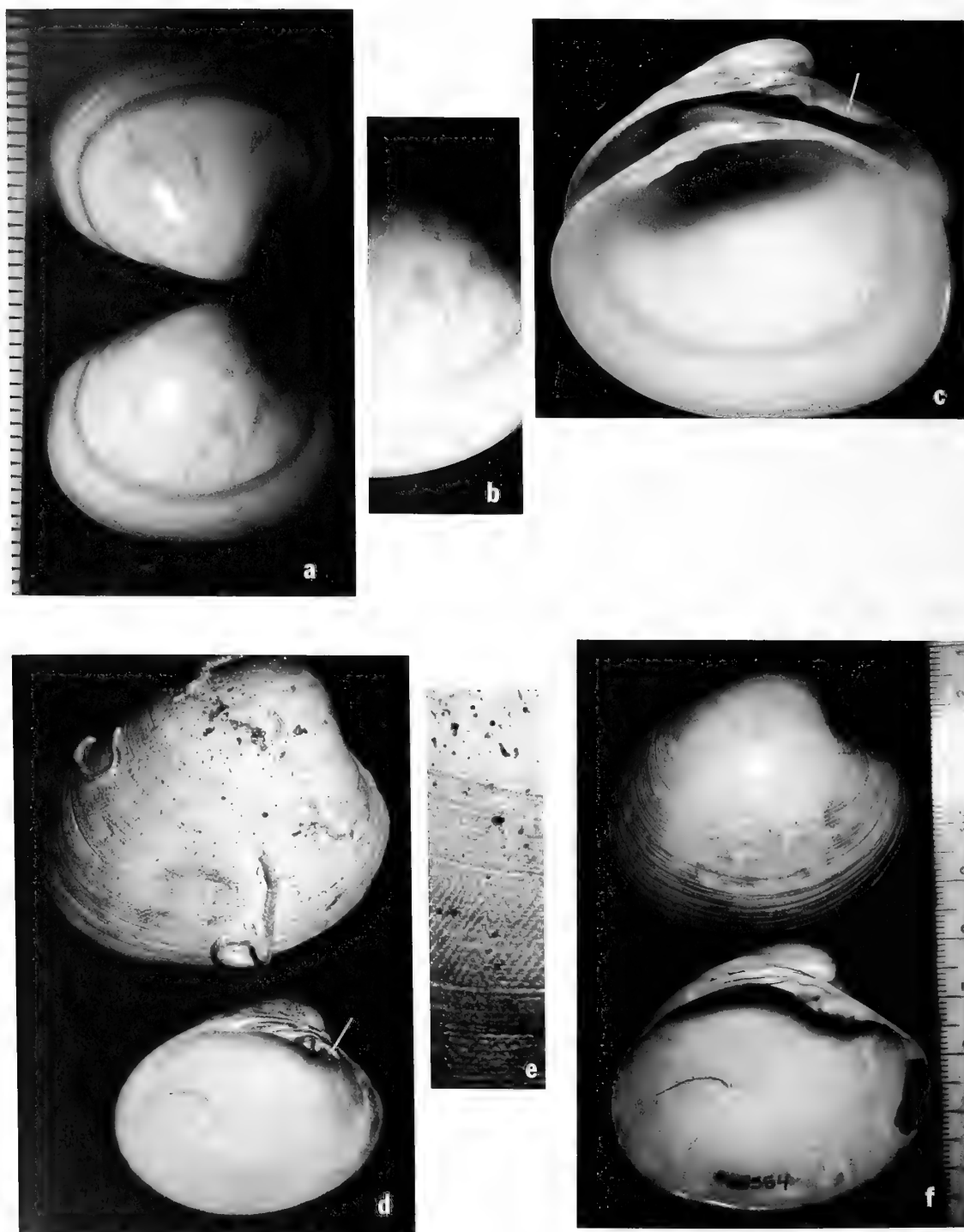


Figure 3

a–c. *Pitar (Hyphantosoma) festoui* sp. nov., Tahiti, Holotype, L = 22 mm. a. Both valves. b. Inset of right valve, showing fine zigzag sculpture. c. Hinge and interior of holotype valves. d, e. *Pitar (H.) intricata* (Dautzenberg), Indonesia. d. Worn valves, L = 53 mm, 38 mm. e. Inset of larger valve, showing fine zigzag sculpture. UCMP specimens. f. *Pitar (H.) aletes* Hertlein & Strong, holotype, CAS 065554.

pronounced and the posterior end is narrower, and more subquadrate. The left anterior lateral of *P. intricata* is closer to the cardinal teeth than that of *P. festoui*.

Type material: Holotype, UCMP 398606.

Type location: Off Afaahiti, Tahiti, French Polynesia (149°15'N, 17°45'W). Two specimens, one of which was subsequently misplaced, were found in coralline sand near clumps of living corals at 60 m, near the end of the water column blue zone.

Key to Recent Species of *Hyphantosoma*

1. Shell from the eastern Pacific 2
1. Shell from the western or central tropical Pacific 3
2. External color patterns absent; if present, pallial sinus nearly half the shell length 4
2. External color patterns obvious; pallial sinus less than half the shell length *hertleini*
3. Umbo rose colored; left anterior lateral well separated from cardinals *festoui*
3. Umbo not rose colored; left anterior lateral situated close to the cardinal *intricata*
4. Pallial sinus less than half the shell length; shell roundly subtrigonal *aletes*
4. Pallial sinus nearly half the shell length; shell ovate *pollicaris*

DISCUSSION

Conchological characteristics link living *Hyphantosoma* closely to American and Pacific species of *Pitar* s. s. The pan-Pacific *Pitar* (*Pitar*) *prora* (Conrad, 1837), for example, has the somewhat well-defined escutcheon and deep, triangular pallial sinus characteristic of *Hyphantosoma* (Figures 2b, 3c, d). *Pitar* (*H.*) *hertleini* has color patterns similar to the eastern Pacific *P. (P.) newcombianus* (Gabb, 1865), and the Caribbean *P. (P.) simpsoni* (Dall, 1889), and *P. (P.) fulminatus* (Menke, 1828). *Pitar hertleini* and *P. fulminatus* have similar hinge plates and pallial sinuses (Figures 2c, d). DALL (1903) linked *P. simpsoni*, marked with zigzags, to *Hyphantosoma* via sculpture, observing that erosion of specimens of *P. simpsoni* revealed zigzag sculpture; how much this might be due to selective erosion of either pigmented or nonpigmented parts of the shell, however, is unknown.

The lunule of *Hyphantosoma* is similar to that of *Pitar* (*Pitarinus*) Rehder & Abbott and *Pitar* (*Pitarella*) Palmer, but the latter two taxa are generally chalky, more obese, and with a well-developed but narrow left anterior lateral tooth. While the restriction of zigzag sculpture within *Pitarinae* to *Hyphantosoma* indicates monophyly, the geographic range of the subgenus and its similarities to both Pacific and Caribbean taxa of *Pitar* allow the possibility of parallel acquisition of zigzag sculpture among those taxa. Anatomical and biomolecular studies could further

clarify the taxonomic relationship of *Hyphantosoma* to the various subgenera of *Pitar*.

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Additions to Pacific Slope Turonian Gastropoda

by

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Abstract. Eighteen species of Pacific Slope Turonian (Late Cretaceous) gastropods are discussed. Nine of the species and six of the genera are new. The new genera are *Praesargana*, *Cydas*, *Saturnus*, *Skyles*, *Varens*, and *Konistra*. The new species are *Anchura* (*Helicaulax*) *tricolor*, *Confusiscala*? *juvenca*, *Confusiscala*? *sulfurea*, *Eripachya* *vaccina*, *Drilluta* *sicca*, *Skyles* *salsus*, *Remera* *vacca*, *Varens* *anae*, and *Varens* *formosus*. The Turonian age of *Palaeatractus crassus* Gabb, 1869, and *Saturnus dubius* (Packard, 1922) is demonstrated. Supraspecific assignment, age, and geographic distribution of *Anchura* (*Helicaulax*) *condoniana* (Anderson, 1902), *Praesargana condoni* (White, 1889), *Cydas crossi* (Anderson, 1958), *Drilluta jacksonensis* (Anderson, 1958), *Carota dilleri* (White, 1889), *Carota*? *mitraeformis* (Gabb, 1869), and *Konistra biconica* (Anderson, 1958) are discussed. Recognition of Gulf Coast and Western Interior genera *Drilluta*, *Remera*, and *Carota* for the first time in Pacific Slope faunas adds to the probability of greater interchange than previously recognized between the Gulf Coast-Western Interior and the Pacific Slope during the Turonian.

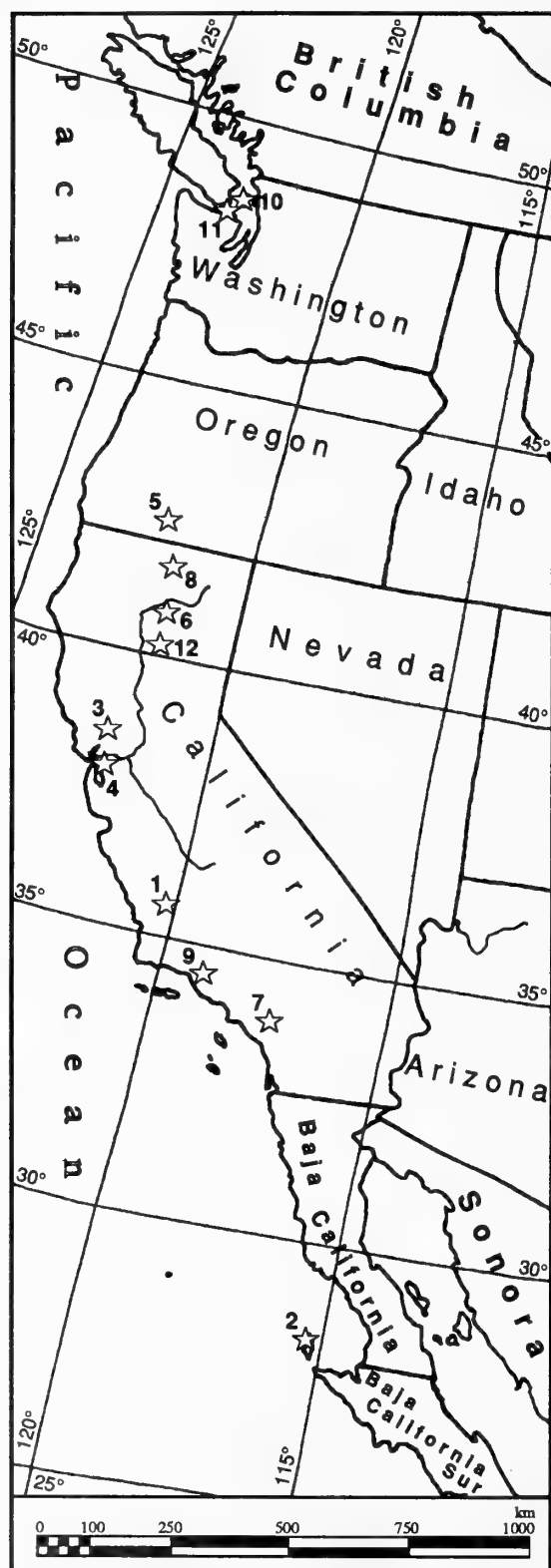
INTRODUCTION

Pacific Slope molluscan faunas of Cretaceous age remain underdescribed. W. P. Popenoe worked on the rich Cretaceous fauna of the Redding area, Shasta County, California (Figure 1), for roughly 50 years. He was particularly interested in gastropods of Turonian age and left at his death unpublished descriptions of a number of species. This paper describes or discusses 18 species, nine of which are new, and proposes six new genera. Although these descriptions are from an uncompleted manuscript on the Redding area, not all of the specimens discussed are from there. Figure 1 is an orientation map for places of occurrence. New taxa proposed are: *Anchura* (*Helicaulax*) *tricolor* sp. nov., *Confusiscala*? *juvenca* sp. nov., *Confusiscala*? *sulfurea* sp. nov., *Praesargana condoni* (White, 1889) gen. nov., *Cydas crossi* (Anderson, 1958) gen. nov., *Eripachya vaccinus* sp. nov., *Saturnus dubius* (Packard, 1922) gen. nov., *Drilluta sicca* sp. nov., *Skyles salsus* gen. et sp. nov.,

Remera vacca sp. nov., *Varens anae* gen. et sp. nov., *Varens formosus* gen. et sp. nov., and *Konistra biconica* (Anderson, 1958) gen. nov. Systematic and stratigraphic position and geographic distribution are discussed for *Anchura* (*Helicaulax*) *condoniana* Anderson, 1902, *Palaeatractus crassus* Gabb, 1869, *Drilluta jacksonensis* (Anderson, 1958), *Carota dilleri* (White, 1889), and *Carota*? *mitraeformis* (Gabb, 1869). *Palaeatractus crassus* Gabb, 1869, "*Cordiera*" *mitraeformis* Gabb, 1869, *Acteon politus* Gabb, 1869, and *Liocium punctatum* Gabb, 1869, were originally described "From the Shasta Group, from a canyon in the foothills, a mile south of the road from Colusa to the Sulphur Springs near the eastern margin of the Coast Range, Colusa County," and considered by GABB (1869) to be of Early Cretaceous age. All four have, however, been collected from beds of Turonian age in the Redding Formation.

Pacific Slope Cretaceous gastropod faunas show, in general, little similarity to faunas of the Gulf Coast and Western Interior, but generic affinities of the Pacific Slope Senonian gastropods to those of Japan have commonly been

¹ Deceased.



recognized. However, among the 13 Turonian genera discussed in this paper, four are also present in the Gulf Coast-Western Interior and a fifth, *Praesargana*, bears strong resemblance to a Gulf Coast genus. These gastropods thus suggest greater interchange with Atlantic realm faunas during the Turonian than during the Senonian. Quantitative comparisons of these faunas must await more complete description of the Pacific Slope faunas. In addition to increasing the knowledge of the paleogeographic distributions of some groups, the descriptions of these Turonian forms increase our ability to assess biodiversity of the past.

Curatorial abbreviations used are CASG = California Academy of Sciences, Geology; CIT = California Institute of Technology; CSMB = California State Mining Bureau; GSC = Geological Survey of Canada; LACM = Natural History Museum of Los Angeles County, Malacology Section; LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; MCZ = Harvard University, Museum of Comparative Zoology; UCBMP = University of California, Berkeley, Museum of Paleontology; UCLA = University of California, Los Angeles, Department of Earth and Space Sciences; UCR = University of California, Riverside, Department of Geological Sciences; USGS = United States Geological Survey; USNM = United States National Museum; UW = University of Washington, Thomas Burke Museum.

In the following descriptions, species characterized as small are under 20 mm in height; those characterized as medium-sized range between 20 mm and 60 mm in height; and those characterized as large are 60 mm or more in height.

Features measured are listed by the following abbreviations in tables: height = H; maximum diameter = D; height of penultimate whorl = Hp; diameter of penultimate whorl = Dp; height of spire = Ha; height of shoulder on penultimate whorl = Hs; length of extended outer lip in aporrhoids = Lw; length of prong in aporrhoids = Lp;

Figure 1

Index map. Two sequences have provided the bulk of the studied material: the exposures of the Redding Formation, northeast of Redding, Shasta Co., and the lower part of the Ladd Formation in the northern Santa Ana Mountains, Orange Co., California. A third significant unit is the Osburger Gulch Member of the Hornbrook Formation cropping out in Jackson Co., Oregon, and Siskiyou Co., California. Place names (starred) mentioned in the text are: 1, Antelope Valley, Kern Co., California; 2, Cedros Island, Baja California, Mexico; 3, Colusa to the Sulphur Springs, Colusa Co., California; 4, Martinez, Contra Costa Co., California; 5, Phoenix, Jackson Co., Oregon; 6, Redding, Shasta Co., California; 7, Santa Ana Mts., Orange Co., California; 8, Siskiyou Co., California; 9, Simi Hills, Los Angeles Co., California; 10, Sucia Island, San Juan Co., Washington; 11, Sydney Island, Straits of Georgia, British Columbia; 12, Tuscan Springs, Tehama Co., California.

length of aperture = La; length of rostrum = Lr; pleural angle = A; number of axial ribs per whorl = R.

SYSTEMATIC PALEONTOLOGY

Phylum Mollusca Linnaeus, 1758

Class Gastropoda Cuvier, 1797

Order Mesogastropoda Wenz, 1938

Superfamily Strombacea Rafinesque, 1815

Family APORRHAIIDAE Gray, 1850

Aporrhaid shells have an aperture with at least three large sinus areas that are independent of the lip extensions. One is posterior and adjacent to the whorl, the second bends the outer lip next to the rostrum, and the third is a hollow across the base of the columella and whorl base that exits on the body side of the anterior rostrum. When the animal is in living position, these sinuses accommodate the head and foot of the animal beneath the shell (Figure 2). The depth of the basal sinus (Figure 2C) is accentuated in some aporrhaid shells by the buildup of callus on the apertural face of the last whorl. In Campanian and Maastrichtian *Anchura* spp. these calluses are commonly very thick, but in the Turonian *Helicaulax* spp. the inner lip is thin to thick and not expanded onto the face of the last whorl.

Genus *Anchura* Conrad, 1860

Type species: *Anchura abrupta* Conrad, 1860, by monotypy, from the Gulf Coast Maastrichtian.

Diagnosis: Medium- to large-sized aporrhaid shells with high, evenly tapering spires; sculpture ornate, with both axial and spiral elements, commonly noded at intersections; aperture sublenticular; anterior rostrum long and narrow; outer lip elongate, extended into a falcate digitation, bent posteriorly.

Subgenus *Anchura* Conrad, 1860

Diagnosis: *Anchura* with the long narrow anterior rostrum deflected to the left in apertural view; lateral arm of the outer lip without flanges.

Discussion: Time and geographic ranges of the subgenus *Anchura* are difficult to determine in the absence of more complete studies of various species that have been assigned to it (SOHL, 1960). The subgenus is well represented in beds ranging in age from Cenomanian through Maastrichtian of North America and Europe. It appears to have a longer range and be more prolific in the Western Interior and the Gulf Coast than elsewhere. On the Pacific Slope it has not yet been found earlier than Turonian. Two Pacific Slope species have been described, *Anchura* (*Anchura*) *falciformis* (Gabb, 1864) of early Campanian age and *A. (A.) gibbera* Webster, 1983, of early Maastrichtian age. Although "*Anchura*" *angulata* (Gabb, 1864) of ?Al-

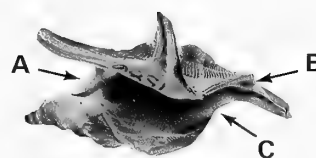


Figure 2

Three large sinus areas of the aporrhaid aperture. A. Posterior sinus to accommodate the posterior part of the foot. B. Anterior outer lip sinus to accommodate the snout. C. Basal sinus to accommodate the anterior part of the foot. (Example is modern *Aporrhais pespelecani* (Linnaeus, 1758) from the Mediterranean Sea, LACM 149737x (= UCLA cat. no. 41586).

bian-Cenomanian age resembles *Anchura* in overall shape, it has a wing more like that of *Drepanochilus* Meek, 1864, or *Dimorphosoma* Gardner, 1875, and very fine sculpture on the spire that is distinctly different than the ornate sculpture of typical *Anchura*.

Subgenus *Helicaulax* Gabb, 1868

Type species: *Rostellaria ornata* d'Orbigny, 1843, by subsequent designation (COSSMANN, 1904), from the Turonian of France.

Diagnosis: Medium-sized, high-spired aporrhaid shells with whorls ornately sculptured by both axial and spiral elements and usually noded at the intersections; last whorl uniangulate; anterior rostrum elongate, narrow, straight; aperture subquadrate; posterior digitation reflexed, elongate, and adnate to spire at its base; outer lip extended, falcate, tapering posteriorly to a spike; inner lip thin to thick.

Discussion: *Helicaulax* resembles *Anchura* Conrad, 1860, in spire, sculpture, rostrum, and expansion of the outer lip, but it differs from *Anchura* in having, in addition to its expanded outer lip, an elongate, reflexed posterior digitation that is adnate to the spire (SOHL, 1960:103). In typical *Anchura* the anterior rostrum is deflected to the left in apertural view, but in *Helicaulax* it is straight. *Helicaulax* tends to develop flanges along the lateral segment of the outer lip. Although GABB (1868), when proposing the subgenus, placed two California species, in addition to the type species, in *Helicaulax*, neither of these California species can be retained in it (SOHL, 1960). *Helicaulax bicarinata* Gabb, 1864, of ?Albian age, is a *Tessarolax* Gabb, 1864, and *H. costata* Gabb, 1864, of Paleocene age is, according to STEWART (1927), an *Araeodactylus* Harris & Burrows, 1891. The chronologic range of *Helicaulax* is Cenomanian to Maastrichtian (SOHL, 1960). *Anchura* (*Helicaulax*) *condoniana* and *A. (H.) tricola* are the only known Pacific Slope representatives of this subgenus, which is better known from the Western Interior and Gulf Coast of North America and from Europe. Whereas *Anchura* (*Anchura*) is more common in North American Upper Cretaceous deposits, *A. (Helicaulax)* is better represented in Europe.

Both *A. (H.) condoniana* and *A. (H.) tricos*a differ from the typical European forms in having the posterior digitation that sprouts adjacent to the whorl, thereafter unattached rather than adnate for part of its length. Additionally, the inner lip of these West Coast species is thick whereas that of *A. (H.) ornata* is very thin (COSSMANN, 1904:64). *Helicaulax* has been considered a subgenus of *Aporrhais* da Costa, 1778, by COSSMANN (1904) and WENZ (1940), but it differs from *Aporrhais* in having a laterally extended falcate outer lip that tapers to a spike rather than the broadly palmate digitated wing of *Aporrhais*. In *Aporrhais* the ornamentation tends to have a bicarinate orientation, but on *Helicaulax* and *Anchura* the complex sculpture has axial and spiral elements that commonly form nodes at intersections. On the last whorl, one or two of the spirals increase in strength to give the body whorl an unicarinate profile. Although *Helicaulax* differs from *Anchura* in having (1) a posterior digitation, (2) flanges along the lateral extension of the wing, (3) a straight anterior rostrum, *Helicaulax* is so similar to *Anchura* Conrad, 1860, that the two must be closely related. Of the two Pacific Slope species, *Anchura (Helicaulax) condoniana* has more poorly developed flanges along the wing and a shorter posterior prong that is late to develop and then callused over. It appears, thus, to be more similar to *Anchura* than is *A. (H.) tricos*a. Except for its posterior digitation and straight anterior rostrum, *A. (H.) condoniana* is similar to *Anchura*. SOHL (1960:106) gives the range of *Anchura* as Cenomanian through Maastrichtian, and includes *Anchura turricula* Stephenson, 1952, from the Cenomanian age Woodbine of Texas despite its slight flanges on the lateral extension of the wing. The morphologies of both *A. (H.) condoniana* and *A. turricula* appear transitional between *A. (Helicaulax)* and *A. (Anchura)*.

The two Pacific Slope Turonian species of *Anchura (Helicaulax)* have different known geographic and sediment distributions. *Anchura (H.) condoniana* has a more northern distribution in sandstone; *A. (H.) tricos*a has a more southern distribution in siltstone. Some of the morphological features of *A. (H.) tricos*a, especially the long posterior prong and the expanded flanges on the lateral

extension of the wing, seem appropriate to a quiet-water habitat on a fine-grained substrate, and the retrieval of these two species from different sediment types is probably related to their ecologic preferences. At present, the significance of the north-south distributions of these two species cannot be determined.

Anchura (Helicaulax) condoniana (Anderson, 1902)

(Figures 3–18)

Anchura condoniana ANDERSON, 1902:76, pl. 8, fig. 179; JONES, SLITER & POPENOE, 1978:xxii.9, pl. 1, fig. 15. Not *Anchura condoniana* Anderson of STADUM, 1973, cover photo = *A. (H.) tricos*a sp. nov.

Drepanochilus condoniana (Anderson): ANDERSON, 1958:166.

Diagnosis: A *Helicaulax* having a short posterior digitation roughly parallel to the shell axis, adjacent to the spire at its base, but not otherwise adnate; sculpture dominantly axial; fifth and sixth abapical spiral cords forming the angulation and continuing onto extended outer lip; outer lip falcate but only slightly flanged posteriorly and anteriorly along its lateral portion.

Description: Shell medium sized, high spired, turriculate, drawn out anteriorly into a moderately long, nearly straight anterior rostrum; whorls about eight in number, barely convex; suture appressed; protoconch unknown; growth line antispirally concave on the spire. Sculpture ornate, consisting of axial and spiral elements, the axial dominant on whorl sides; surface of spire ornamented by about 20 slightly arcuate axial ribs crossed by six spiral ribs forming nodes at axial-spiral intersections; the first four abapical ribs separated by interspaces of nearly equal width, the fifth, sixth, and seventh closer together, the fifth and sixth forming the peripheral angulation on the last whorl and continuing onto the extended outer lip. Aperture subquadrate, deeply broadly sinused between posterior spur and falcate digitation; outer lip with two extensions, a short straight, spurlike process adjacent to the spire and a long and falcate digitation, slightly flanged both posteriorly and anteriorly along its lateral portion, and grooved internally

Explanation of Figures 3 to 18

All figures $\times 1$; all specimens, except LACMIP cat. no. 11537, coated with ammonium chloride.

Figures 3–10. *Anchura (Helicaulax) condoniana* Anderson, 1902. Figure 3: LACMIP cat. no. 10837 from UCLA loc. 4214, holotype, apertural view. Figure 4: CAS cat. no. 445.30 from CAS loc. 445, holotype, back view. Figures 5–8: LACMIP cat. no. 11540 from LACMIP loc. 10735, hypotype; Figure 5, right side; Figure 6, back; Figure 8, aperture. Figure 7: LACMIP cat. no. 11539 (latex pull) from LACMIP loc. 10735, hypotype, aperture. Figure 9: LACMIP cat. no. 11537 (latex pull) from LACMIP loc. 10726, hypotype, back, apparent bend in rostrum results from imperfection in rock mold. Figure 10: LACMIP cat. no. 11538 from UCLA loc. 4214, hypotype, back.

Figures 11–18. *Anchura (Helicaulax) tricos*a sp. nov. Figure 11: USNM cat. no. 465514 from USGS loc. 2759, holotype, aperture. Figure 12: USNM cat. no. 465515 from USGS loc. 2759, paratype, back. Figure 13: Paratype, USNM cat. no. 465518 from USGS loc. 2757, back. Figures 14, 15: USNM cat. no. 465517 from USGS loc. 2757, paratype; Figure 14, aperture; Figure 15, back. Figure 16: UCR cat. no. 7787/101 from UCR loc. 7787, paratype, aperture. Figure 17: LACMIP cat. no. 11541 from UCLA loc. 4235, paratype, back. Figure 18: Chapman College specimen figured by STADUM (1973) from Ladd Formation, upper Holz Shale Member, Santa Ana Mts., California, paratype, collected and prepared by Frank and Mabel Grouard. Photographs 3, 9, 10, 18 by Susuki; 4–8, 11–17 by De Leon.

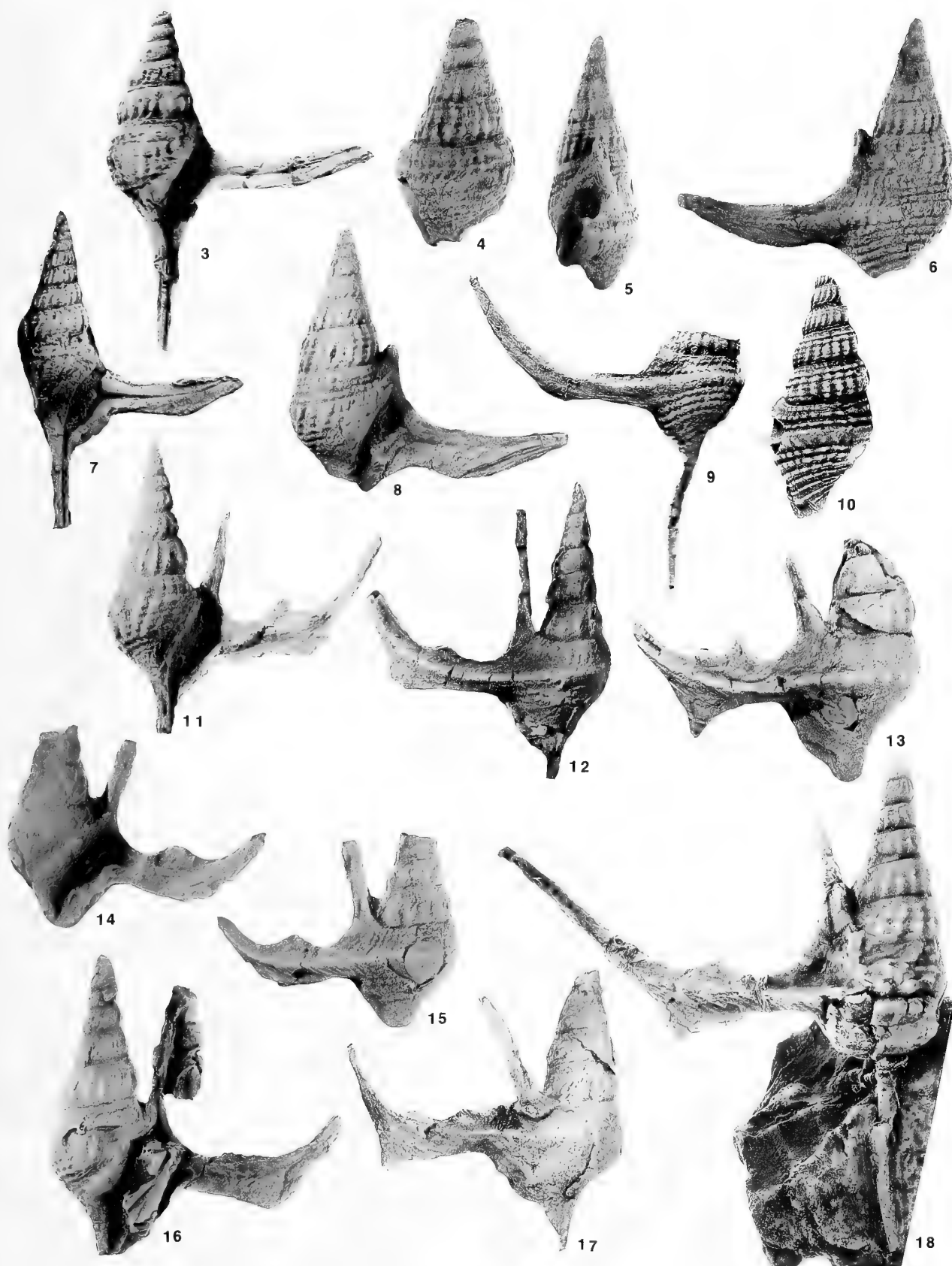


Table 1
Measurements (mm) of *Anchura* (*Helicaulax*) *condoniana* Anderson, 1902.

	H	D	Hp	Dp	Ha	Lw	Lp	A	Lr	Dp/Hp
CAS 445.30	45.0*	23.0	9.0	16.4	25.0	—	—	34°	—	1.8
UCLA 58437	58.7*	17.0†	6.4	14.6†	18.0*	30.0*	—	39°	24.0	2.3
LACMIP 11537●	42.8*	17.4†	7.8	14.8†	23.0*	—	—	35°	—	1.9
LACMIP 11538	41.5*	19.0†	7.0	15.0†	22.8*	—	—	36°	—	2.1
LACMIP 11539●	46.0*	—	—	—	29.0	31.0	11.0	30°	—	—
LACMIP 11540	60.0	—	7.0	—	25.5	26.0	—	—	19.0	—

* Specimen incomplete; † specimen crushed; ● latex pull. Abbreviations decrypted in Introduction.

opposite the external ridge; groove filled by thick callus deposit within aperture; inner lip very thick.

Holotype: CASG cat. no. 445.30.

Hypotypes: LACMIP cat. nos. 10837 (= UCLA 58437), 11538 from LACMIP loc. 24214 (= UCLA loc. 4214), Little Cow Creek; 11537 from LACMIP loc. 10726 (= CIT loc. 1032), Dry Creek; 11539–11540 from LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek, Shasta Co., California.

Dimensions: See Table 1.

Type locality: CASG loc. 445, Forty-nine mine, near Phoenix, Jackson Co., Oregon (Anderson, 1902).

Distribution: Unnamed formation on Sidney Island (coll.: Peter Ward, 3 September 1992), British Columbia; Hornbrook Formation, Jackson Co., Oregon; Hornbrook Formation, Osburger Gulch Member, Siskiyou Co., California; Redding Formation, Bellavista Sandstone Member, rare, Frazier Silt Member, locally abundant, Melton Sandstone Member, rare, northeast of Redding, Shasta Co., California.

Geologic age: Middle to late Turonian, at LACMIP loc. 10876 (= CIT loc. 1042) associated with *Subprionocyclus neptuni* (Geinitz, 1849) (MATSUMOTO, 1960:102).

Remarks: The holotype was rescued from the ashes after the 1906 San Francisco earthquake. It now lacks the expanded wing and the rostrum of ANDERSON's (1902) figure (figure 179).

The extended wing of *Anchura* (*H.*) *condoniana* apparently formed before the posterior prong. Several specimens that have an extended falcate outer lip have no posterior spur (e.g., the specimen figured by JONES *et al.*, 1978:pl. 1, fig. 15) and no indication that one has broken off. Apertures of specimens that have a spur have thicker callus deposits within the aperture, suggesting that these are more mature specimens.

Anchura (*Helicaulax*) *condoniana* differs from the similar *A. (H.) tricososa* in having the prong shorter and at less of an angle to the shell axis, only suggestions of flanges along

the lateral extension of the outer lip, and a sturdier shell. The more strongly noded sculpture of *A. (H.) condoniana* is more similar to that of typical *Helicaulax* than is that of *A. (H.) tricososa*.

PACKARD (1916:148) reported both *Alaria condoniana* and *Alaria falciformis* (Gabb, 1864) from the "Actaeonella oviformis" Zone of the Santa Ana Mountains. "Actaeonella oviformis" in the Santa Ana Mountains is *Trochactaeon* (*T.*) *packardi* (Anderson, 1958) and of Turonian age (SOHL & KOLLMANN, 1985). *Anchura* (*Helicaulax*) *condoniana* is also from the Turonian, but specimens so identified from the Santa Ana Mountains thus far examined are *Anchura* (*Helicaulax*) *tricososa* sp. nov. POPENOE (1942:fig. 4) recorded *Anchura* cf. *A. falciformis* (Gabb, 1864) from nine localities in the Santa Ana Mountains. The specimens from his localities in the Baker Canyon Sandstone and "Holzbaker Transition" are also *A. (H.) tricososa* sp. nov. with the exception of those from LACMIP loc. 10100 (= CIT loc. 92) which are an undescribed new species of *Anchura* (*Anchura*). Popenoe's specimens of *A. cf. A. falciformis* from the upper Holz Shale belong to another undescribed species of *Anchura* (*Anchura*). The *Anchura* (*Helicaulax*) *condoniana* of STADUM (1973) from the Santa Ana Mountains Turonian is an unusually complete specimen of *Anchura* (*Helicaulax*) *tricososa* sp. nov. *Anchura* (*Helicaulax*) *condoniana* is locally abundant in the Redding region, but few specimens have the rostrum and extended outer lip preserved.

Anchura (*Helicaulax*) Saul & Popenoe,
tricososa sp. nov.

(Figures 11–18)

Anchura condoniana Anderson: STADUM, 1973, cover photo.
Not *Anchura condoniana* Anderson, 1902.

Diagnosis: A large-sized *Helicaulax* with a long, posterior prong that is at an angle to the shell axis and a falcate outer lip broadened both anteriorly and posteriorly by angulate flanges.

Description: Shell large, high spired, drawn out anteriorly into a long, straight anterior rostrum; whorls about nine

Table 2
Measurements (mm) of *Anchura (Helicaulax) tricoso* sp. nov.

	H	D	Hp	Dp	Ha	Lw	Lp	A	Lr	Dp/Hp
LACMIP 11541	53.0*	19.7	7.7	14.3	25.0*	31.0	22.0	30°	13.8*	1.8
LACMIP 11542	43.7*	19.5	8.8	15.8	26.0*	32.5*	10.0*	25°	—	1.8
UCR 7787/101	52.1*	17.0†	7.5	14.7†	25.7	33.3*	19.0	28°	—	2.0
USNM 465514	42.0*	16.5	6.8	13.5	24.0*	33.0*	14.0	26°	—	2.0
USNM 465515	50.0*	18.0	6.7	12.0	31.0	45.5*	22.0	22°	8.0*	1.8
USNM 465517	37.0*	16.0	8.0	12.6	15.0*	29.6*	16.0	27°	—	1.6
USNM 465518	45.0*	21.0	9.0	15.8	19.0*	35.7*	14.5*	—	10.0*	1.8

* Specimen incomplete; † specimen crushed. Abbreviations decrypted in Introduction.

in number, wider than high, barely convex; suture impressed; body whorl angulate; anterior rostrum longer than the last whorl, slender, straight; early whorls with arcuate axial ribs; penultimate whorl ornamented by about 16 axial ribs crossed by straplike spiral ribs, about five on the spire and eight or nine on the body whorl; ribs forming nodes at intersections; first three abapical ribs separated by slightly wider interspaces, fourth and fifth closer together, forming the angulation of the body whorl that extends onto the outer lip digitation. Aperture subtriangular, deeply broadly sinused between posterior spur and falcate digitation; outer lip with two extensions, a relatively long, straight, spurlike posterior process basally adjacent to the spire and a long, and falcate digitation flanged both posteriorly and anteriorly along its lateral extension; posterior prong at an angle of 20°–30° to the shell axis.

Holotype: USNM cat. no. 465514.

Paratypes: LACMIP cat. nos. 11541 from UCLA loc. 4235, Holz Ranch, and 11542 from LACMIP loc. 15295, Silverado Canyon, Santa Ana Mts., Orange Co., California; UCR cat. nos. 7787/101, from UCR loc. 7787, Silverado Canyon, and 7788/20, from UCR loc. 7788, Silverado Canyon, Santa Ana Mts., Orange Co., California; USNM cat. nos. 465517–465518 from USGS loc. 2757, Silverado Canyon; USNM cat. nos. 465515–465516 from USGS loc. 2759, Ladd Canyon, Santa Ana Mts., Orange Co., California; Stadum specimen.

Type locality: USGS loc. 2759, lower Ladd Canyon, near Silverado Canyon, Santa Ana Mts., Orange Co., California.

Dimensions: See Table 2.

Distribution: Ladd Formation, upper Baker Canyon Sandstone and lower Holz Shale members, uncommon, Santa Ana Mts., Orange Co., California.

Geologic age: Turonian.

Remarks: *Anchura (Helicaulax) tricoso* differs from *A. (H.) condoniana* in having a broader falcate outer lip with

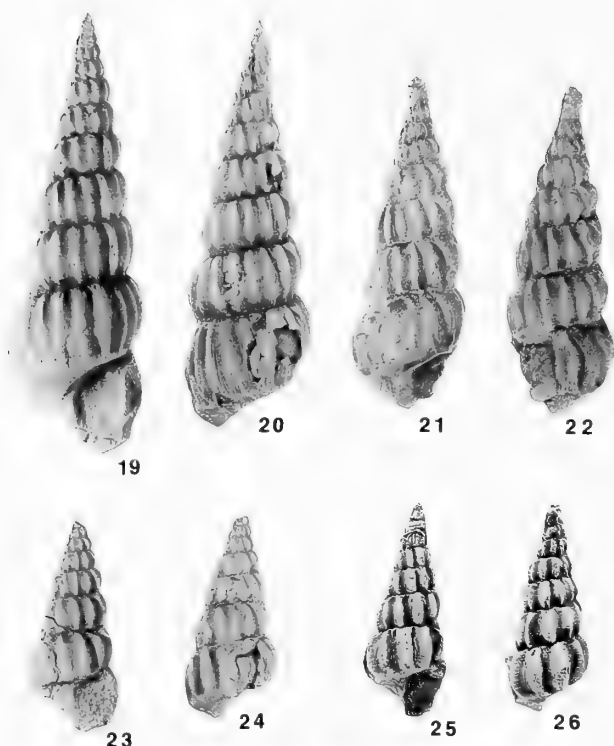
angulately developed flanges, a longer posterior spur that extends at a greater angle to the shell axis, fewer axial ribs on the spire, a narrower pleural angle, and a slightly taller spire. On most available specimens, both axial and spiral sculpture appear more subdued than on *A. (H.) condoniana*, but this is at least partly due to preservation. A few specimens (e.g., the holotype and paratypes UCR 7788/101–102) have the sculpture fairly well preserved. On these *A. (H.) tricoso*, the spirals are narrower and the interspirals wider, the axials fewer, and the nodes at the intersection stronger, especially on the angulation, than on *A. (H.) condoniana*. *Anchura (H.) tricoso* is from fine-grained muddy sandstone and siltstone, but *A. (H.) condoniana* is common in beds of coarser grain. A fragmentary specimen (USNM cat. no. 465516) of *A. (H.) tricoso* has a body whorl diameter of about 20 mm, suggesting a height of at least 72 mm, a size close to twice that of any *A. (H.) condoniana*. As discussed under *A. (H.) condoniana*, PACKARD's (1916) *Alaria condoniana* from the Santa Ana Mountains is *Anchura (H.) tricoso* as is POPENOE's (1942) *Anchura* cf. *A. falciformis* from the upper Baker Canyon Sandstone and lower Holz Shale members of the Ladd Formation. POPENOE's (1942) specimens of *A. cf. A. falciformis* from the upper Holz Shale differ from *A. (H.) tricoso* in lacking the posterior prong, in having a shorter lateral extension to the wing that lacks flanges, and in being more coarsely sculptured. USNM 465515 was encrusted with calcareous tubes (probably annelid) on both apertural and abapertural sides of the wing and on the base of the body whorl adjacent to the lip. These encrustations were probably subsequent to the death of the gastropod.

Etymology: The species name is from the Latin *tricosus*, meaning full of tricks or wiles.

Superfamily ?JANTHINACEA, Lamarck, 1812

Family EPITONIIDAE Berry, 1910

SOHL (1964) placed the Epitoniidae in the order Cephalaspidea, but PONDER & WARÉN (1988) have included it in



Explanation of Figures 19 to 26

All figures $\times 1$; all specimens coated with ammonium chloride.

Figures 19–24. *Confusiscula? sulfurea* sp. nov. Figures 19, 20: CAS cat. no. 66549.01 from CAS loc. 66549, holotype; Figure 19, aperture; Figure 20, back. Figures 21, 22: LACMIP cat. no. 11544 from UCLA loc. 7233, paratype; Figure 21, apertural side; Figure 22, back. Figures 23, 24: LACMIP cat. no. 11545 from UCLA loc. 4252, paratype; Figure 23, aperture; Figure 24, back.

Figures 25, 26. *Confusiscula? juvenca* sp. nov. Figures 25, 26: LACMIP cat. no. 11543 from LACMIP loc. 10735, holotype; Figure 25, apertural side; Figure 26, back. Photographs, 19–24 by De Leon; 25, 26 by Susuki.

the superfamily Janthinoidea, Lamarck, 1812, which they place near the end of the Mesogastropoda.

Genus *Confusiscula* de Boury, 1909

Type species: by original designation and monotypy, *Scalaria dupiniana* d'Orbigny, 1842, from Aube, France, of Albian age.

Confusiscula was originally considered to be a subgenus of *Amaea* by DE BOURY (1909). It has continued to be treated as a subgenus by several workers, including STEWART (1927), who placed it as a subgenus of *Epitonium* Röding, 1798, WENZ (1940) as a subgenus of *Amaea* H. & A. Adams, 1853, and DURHAM (1937) as a subgenus of *Opalia* H. & A. Adams, 1853. GARDNER (1876) had included *Scalaria dupiniana* and its allies in *Opalia*, and

the two species described here resemble *Opalia*. *Confusiscula? juvenca* is as similar to *Opalia* as to *Confusiscula*.

COSSMANN (1912:73) considered *Confusiscula* a full genus and characterized it as having axial ribs and varices that do not cross the basal cord, which is visible on the spire supradjacent to the suture. The axial ribs are not always aligned with ribs of adjacent whorls, and they are posteriorly somewhat reflected toward the basal cord. Whorl sides are completely overrun by fine spiral threads. The base is rather flat and circumscribed peripherally by the somewhat projecting basal cord against which the axial ribs abut. The basal disk is ornamented by fine spiral threads and crossed by radiating slightly sinuous growth lines. The aperture has a small posterior canal against the basal cord of the penultimate whorl.

COSSMANN (1912) listed occurrences of species referred to *Confusiscula* from nearly all continents, but the genus has apparently not been recognized in the Western Interior, Atlantic, and Gulf Coast Cretaceous faunas of the United States. The genus ranges from Neocomian (GARDNER, 1876) through Maastrichtian.

Confusiscula? sulfurea Saul & Popenoe, sp. nov.

(Figures 19–24)

Opalia (Confusiscula) mathewsonii (Gabb)? : DURHAM, 1937: 504, pl. 56, fig. 23.

Diagnosis: A medium-sized *Confusiscula* with axial ribs that extend from suture to basal cord and increase gradually in number, 12 on the fifth whorl and 19 on the 12th whorl; basal cord variably exposed on spire.

Description: Shell medium sized, turreted; pleural angle about 24° ; whorls 12, moderately convex, width more than twice height; sutures impressed, not always anterior to the basal cord; basal disk flattened, bordered peripherally by a strong cord and centrally by a low swelling about an indistinct umbilical depression. Whorl sides sculptured by strong, scarcely sigmoid, swollen, round crested axial ribs, overridden by fine spiral threads; ribs just reaching the posterior suture and terminating at the basal cord, nearly aligned with ribs of adjacent whorls, but not confluent, 12 ribs on fifth whorl, 19 ribs on twelfth whorl; rib interspaces round bottomed, about equal in width to the ribs; spiral sculpture of low, spaced, spiral threads of alternating strength; base with fine more closely spaced nearly equal spiral threads; growth line a little prosocline at the suture, broadly barely concave medially. Aperture subquadrate; inner lip narrow, a little thickened.

Holotype: CASG cat. no. 66549.01 (= CASG cat. no. 7010, DURHAM, 1937:pl. 56, fig. 23)

Paratypes: LACMIP cat. no. 11545 from UCLA loc. 4252, Ashland, Oregon; and 11544 from UCLA loc. 7233, Sulphur Creek, Redding quadrangle, Shasta Co., California.

Dimensions: See Table 3.

Type locality: CASG loc. 66549, Hagerdorn Ranch, 4 miles (6.4 km) northwest of Montague, Siskiyou Co., California.

Distribution: Hornbrook Formation, ?Osburger Gulch Member, near Ashland, Jackson Co., Oregon; Hornbrook Formation, ?Osburger Gulch Member, near Montague, Siskiyou Co.; Redding Formation, Bellavista Sandstone Member, Redding area, Shasta Co., California.

Geologic age: Turonian.

Remarks: Three species resembling *Confusiscala* have been described from the Pacific Slope Cretaceous faunas. The first of these, "*Scalaria*" *mathewsonii* Gabb, 1864, was referred to *Confusiscala* by STEWART (1927). It is based on a single, poorly preserved specimen consisting of four incomplete, partially exposed whorls, from "near Martinez," Contra Costa Co., California. Deposits "near Martinez" range in age from Albion to Maastrichtian. Preservation of the holotype of "*S.*" *mathewsonii* suggests that it is of Maastrichtian age. In *C.?* *sulfurea* the basal cord is less strong, the whorls are less convex, and the axial ribs are narrower with comparatively wider interspaces. If STEWART's (1927) estimate that *C.?* *mathewsonii* had about 12 axial ribs is correct, *C.?* *sulfurea* has the greater number of ribs.

The second species is *Mesostoma* (?) *newcombii* Whittes, 1903, from the Cedar District Formation of Sucia Island, San Juan Co., Washington. It is Campanian in age and differs from *Confusiscala?* *sulfurea* in its much larger size and relatively shorter whorl height. In *C. newcombii* axial ribs fade toward the posterior suture, creating a whorl profile that is broadest near its base, whereas *C.?* *sulfurea* has longer ribs and a more evenly rounded whorl profile.

The third and even larger species is *Cerithium suciense* Packard, 1922, described from a specimen consisting of two whorls (height 59 mm, diameter 44 mm) probably from the Cedar District Formation on Sucia Island, San Juan Co., Washington (UCB loc. 2209), which is of mid Campanian age. Another and larger specimen consisting of eight whorls (height incomplete 162 mm, diameter 56 mm) is available from that part of the Chatsworth Formation in the Simi Hills yielding *Metaplaenticeras* aff. *M. pacificum* (Smith, 1900). *Confusiscala suciense* is from the *Hoplitoplaenticeras vancouverense* to *Metaplaenticeras pacificum* zones and of mid to late Campanian age. *Confusiscala?* *sulfurea* is much smaller than *C. suciense* and lacks the strong posterior growth line sinus just subjacent to the suture.

The holotype of *Confusiscala?* *sulfurea* was described as being "from the upper Chico beds," reflecting common usage 60 years ago, but the Cretaceous strata near Montague are now referred to as the Hornbrook Formation. Present in the matrix of the holotype are specimens of

Table 3

Measurements (mm) of *Confusiscala?* *sulfurea* sp. nov. and *C.?* *juvenca* sp. nov.

	H	D	Hp	Dp	A	R	Dp/ Hp
<i>C.?</i> <i>sulfurea</i>							
CASG 66549.01	51.3	19.0	8.5	14.4	22°	19	1.7
LACMIP 11544	45.8	14.6†	7.5	9.4†	21°	13	1.2
LACMIP 11545	27.2	12.5	5.6	10.5†	26°	13	1.9
<i>C.?</i> <i>juvenca</i>							
LACMIP 11543	27.4	10.9	5.0	8.9	31°	10	1.8

* Specimen incomplete; † specimen crushed. Abbreviations de-crypted in Introduction.

Turritella hearni Merriam, 1941, a species of Turonian age that is present in the lower Hornbrook Formation.

Confusiscala? *sulfurea* is not a typical *Confusiscala*. Its axial ribs, like those of *C.?* *mathewsonii*, extend from the posterior suture to the basal cord, and it differs from *C. dupiniana* in having longer axial ribs and a more evenly rounded whorl profile.

Etymology: The species name *sulfurea* is Latin and refers to the occurrence of this species on Sulphur Creek, Shasta Co., California.

Confusiscala? *juvenca* Saul & Popenoe, sp. nov.

(Figures 25, 26)

Diagnosis: An *Opalia*-like epitoniid with 10 to 12 strong, shouldered axial ribs per whorl and a strong basal disk; whorls overlain with fine cancellate sculpture produced by fine spiral threads and growth lines.

Description: Shell of medium size, turreted; pleural angle about 30°; whorls eight or nine in number, moderately convex, width about twice height; sutures deeply impressed; basal disk flattened, a little concave, bordered peripherally by a thick and rounded cord; no umbilicus. Whorl sides sculptured; axial sculpture of 10 to 12 nearly straight, slightly oblique, swollen, round-crested ribs, shouldered at the posterior suture, abruptly terminating at the basal cord, and nearly or quite in alignment with the ribs of adjacent whorls, but not confluent; rib interspaces round bottomed, equal in width to the ribs; spiral sculpture of low, faint, rather widely spaced spiral threads alternating with finer spiral threads and crossed by growth lines producing an overall finely cancellate appearance, extending over the basal disk; growth line with a shallow (about equal to ½ the axial rib thickness) but well-marked sinus at the shoulder. Aperture probably almost quadrate with a spoutlike extension at its inner anterior border and a posterior notch at the shoulder; inner lip thin, narrow, reflected onto base; outer lip unknown.

Holotype: LACMIP cat. no. 11543.

Dimensions: See Table 3.

Type locality: LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek, 2 miles (3.2 km) NE of Frazier Corners, Shasta Co., California.

Distribution: Redding Formation, Frazier Siltstone Member, Redding area, Shasta Co., California.

Geologic age: Turonian.

Remarks: *Confusiscala? juvenca* differs from *C.? sulfurea* in having strongly shouldered and straighter axial ribs, fewer, more irregular spirals on its basal disk, a posterior growth line sinus, and the suture posterior to the basal cord so that the basal cord does not show on the spire. In *C.? juvenca* the growth line has a posterior notch like that of *C. suciensis*, but the ribs are much straighter and longer, extending from the shoulder to the basal cord without diminished strength.

Confusiscala? juvenca has many of the characteristics of the genus *Opalia* (type species *Opalia australis* (Lamarck, 1822)), but differs in at least two respects: *C.? juvenca* has a well-marked but shallow posterior sinus to the growth line at the shoulder, and *C.? juvenca* apparently lacks the spiral bands of punctations of *Opalia*. Although the holotype of *C.? juvenca* appears well preserved, recrystallization and mineralization of the specimen may have obscured some details, and such details as punctations could be obscured. This species is geologically older and more strongly shouldered than the Maastrichtian, Gulf Coast species assigned to *Opalia* by SOHL (1964).

Etymology: The species name *juvenca* is Latin, meaning young, and refers to the occurrence of this species in the Little Cow Creek drainage.

Order NEOGASTROPODA Thiele, 1929

Superfamily MURICACEA Rafinesque, 1815

Family SARGANIDAE Stephenson, 1923

STEPHENSON (1923) proposed the new family Sarganidae to contain *Sargana* Stephenson, 1923, distinguishing it from Muricidae on the basis of the columellar folds and the flattened spire. SOHL (1964:173) and WENZ (1941:1082) have placed *Sargana* in the subfamily Rapaninae of the family Muricidae, but PONDER & WARÉN (1988) included Rapaninae in the Thaidinae and recognize Sarganinae. The placement of *Sargana* and of Sarganinae in Muricidae is questioned by GARVIE (1991), who quotes uncompleted work on protoconchs by Klaus Bandel as indicating that *Sargana* is a close relative of *Trichotropis*, and this placement was abrogated by GARVIE (1992), who places *Sargana* without attribution or mention of morphological criteria in the Cancellariidae. The spiny shell of *Sargana* does not resemble that of *Trichotropis*. In several features—pyriform shape, flattened protoconch, complex spiny sculpture—*Sargana* resembles *Pyropsis* Conrad, 1860, which

STEPHENSON (1941) placed in the Pyropsidae. SOHL (1964) considered the separation of the Pyropsidae as a family too drastic and left it in the Vasidae H. & A. Adams, 1853, but SAUL (1988) included *Pyropsis* in Tudicidae Cossmann, 1901, placing it in the superfamily Muricacea. In shape and placement of the posterior siphonal notch, the aperture of *Sargana* resembles that of tudicids more than it does that of muricines. The aperture does not resemble that of trichotropids, and unlike the many muricines that have a posterior outer lip sinus at the shoulder rather than against the body whorl, the Sarganidae have a well-developed posterior sinus against the body whorl. The aperture of *Sargana* also differs from that of cancellariids in forming a narrow, constricted anterior canal that is abruptly confined posteriorly, whereas in cancellariids the anterior canal is typically broad and not confined at its apertural junction.

***Praesargana* Saul & Popenoe, gen. nov.**

Type species: *Trophon condoni* White, 1889.

Diagnosis: Small, very low-spined sarganids with moderate, laciniate anterior siphon, and a shallow umbilical depression bounded by a roughened fasciole. Outer lip bearing a tubercle opposite the spiral fold of the inner lip. Siphonal canal short and bent to the left.

Discussion: *Praesargana* lacks the deep spiral sulcus at the base of the body whorl of *Sargana*. It has finer, more regular, and nodular rather than spinose sculpture; a smaller and shallower umbilical depression; and a shorter, straighter and more open siphonal canal than *Sargana*.

The resemblance of *Praesargana* to *Sargana* suggests inclusion of *Praesargana* in the Sarganinae. The protoconch of *Praesargana* is paucispiral, consisting of but two rapidly expanding flattened, carinate whorls. Because the shells are recrystallized and entombed in tenacious, well-cemented matrix, any fine sculpture is as yet unknown. In shell form and sculpture *Praesargana* does not resemble *Trichotropis*. Although its anterior siphonal canal is broader than that of *Sargana*, the anterior canal of *Praesargana* is abruptly confined posteriorly and much narrower than that of cancellariids.

The generic name is compounded of *Sargana*, derived from the Greek *sargane*, meaning braid, plait, basket, and the Latin prefix *Prae*, meaning before, and is of feminine gender.

***Praesargana condoni* (White, 1889)**

(Figures 27–37)

Trophon condoni WHITE, 1889:21, pl. 3, figs. 4–5; ANDERSON, 1958:168; JONES, SLITER & POPENOE, 1978:xxii.9, pl. 1, figs. 8–9.

Diagnosis: As for the genus.

Description: Shell small; spire very low; whorls rapidly expanding, roundly shouldered and convex posteriorly, be-

coming concave on the short broad siphonal neck; anterior end of siphon rounded and laciniate; suture appressed; ramp slightly concave; umbilical depression shallow, narrow, bounded by a roughened fasciole. Protoconch paucispiral, consisting of about two rapidly expanding, carinate whorls surrounding an apical dimple. Sculpture of about 12 strong, evenly spaced, rough, round-topped spiral cords crossed by about 20 nearly straight, collabral ribs, producing a coarse cancellate appearance, strong at the whorl shoulder, diminishing anteriorly, scarcely evident on the basal fourth of the last whorl. Aperture broadly subovate, its two lips, meeting by the thickening of each as the shell approaches maturity, extend back upon the ultimate volution; apertural callus at posterior juncture of inner and outer lips bearing a shallow siphonal groove extending spireward to the shoulder of the penultimate whorl; aperture sharply constricted at its passage into anterior canal by a projecting tubercle on the inner margin of the outer lip, opposing a similarly placed spiral fold on the inner lip; siphonal canal short, narrow, slotlike and strongly bent to the left, margins parallel.

Syntypes: USNM cat. no. 20122 (2 specimens).

Hypotypes: LACMIP cat. no. 10807 (= UCLA cat. no. 58443) from LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek, 2 miles (3.2 km) northeast of Frazier Corners, Shasta Co.; LACMIP cat. no. 11546 from UCLA loc. 5422, Rancheria Gulch, Siskiyou Co.; LACMIP cat. no. 11585 from LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek, Shasta Co.; LACMIP cat. no. 11586 from UCLA loc. 4214, Little Cow Creek, Shasta Co., California.

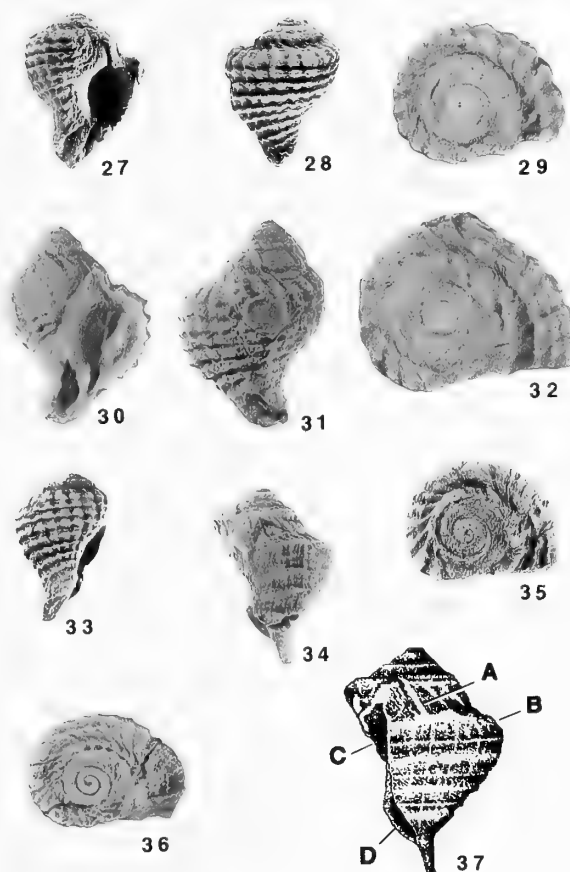
Dimensions: See Table 4.

Type locality: "Chico Group, Little Cow Creek Valley, about eighteen miles [29 km] east of Redding, Shasta County" (WHITE, 1889).

Distribution: Hornbrook Formation, Osburger Gulch Sandstone Member, Rancheria Gulch, Siskiyou Co.; common in sandstone lenses near middle of Frazier Silt Member of Redding Formation, Redding area, Shasta Co., California; reported from "Turonian of Putah Creek, near the Napa-Yolo County line" (ANDERSON, 1958:168).

Geologic age: Turonian.

Remarks: *Praesargana condoni* resembles *Sargana stantoni* (Weller, 1907), type species of *Sargana* from Maastrichtian of Gulf and Atlantic coasts, and *S. geversi* (Rennie, 1930) from Senonian of Pondoland, but *P. condoni* lacks their basal constriction. Its sculpture is less spiny than that of *S. stantoni*, and its protoconch is not as strongly carinate. It has more spiral cords on the ramp than *S. geversi* and fewer than *S. stantoni*. It also resembles "*Rapana*" *tuberculosa* Stoliczka (1868) from the Trichinopoly beds of South India, but differs from this species in its more abruptly constricted last whorl at the beginning of the siphonal



Explanation of Figures 27 to 37

All specimens coated with ammonium chloride; unless otherwise indicated figures are $\times 1$.

Figures 27–37. *Praesargana condoni* (White, 1889). Figures 27–29, 33: LACMIP cat. no. 10807 from LACMIP loc. 10735, hypotype; Figure 27, aperture; Figure 28, back; Figure 29, apical view, $\times 1.5$; Figure 33, left side. Figures 30–32: LACMIP cat. no. 11546 from UCLA loc. 5422, hypotype, specimen with rounded shoulder and higher spire; Figure 30, aperture; Figure 31, back; Figure 32, apical view, $\times 1.5$. Figures 34, 36, 37: LACMIP cat. no. 11586 from UCLA loc. 4214, hypotype; Figure 34, right side, showing bulging portion of last whorl; Figure 36, apical view, higher spired specimen than 11585 (Figure 35) and 10807 (Figures 27–29, 33). Figure 37, computer scan of Figure 34 enhanced through use of Canvas 3.0 to show position of present aperture edge, varix, and former position of posterior canal, $\times 1.33$; A, varix with posterior sinus; B, shoulder; C, aperture; D, umbilical fasciole. Figure 35, LACMIP cat. no. 11585 from LACMIP loc. 10735, hypotype, apical view, showing suppression of axial ribbing and some bulging of whorl on last third of body whorl, $\times 1.5$. Photographs 27, 28 by Susuki; 29–36 by De Leon.

canal. *Praesargana condoni* is geologically older than these three species of *Sargana*.

Praesargana condoni is morphologically variable. The strength of the spiral cords varies from even to irregular with four commonly stronger, the shoulder cord and three alternate anterior cords (Figures 34, 37). The shoulder is

Table 4
Measurements (mm) of *Praesargana condoni* (White, 1889).

	H	D	Hp	Dp	Ha	Hs	A	Dp/Hp	Hp/Hs
UCLA 59443	19.0	15.0	2.0	7.6	3.0	?	114°	3.8	?
LACMIP 11546	27.3	21.2	4.8	8.9	6.5	1.0	88°	4.9	4.8
LACMIP 11585	17.6	16.9	1.8	6.8	3.4	‡	110°	3.8	?
LACMIP 11586	23.7	21.6	3.0	10.5	5.0	1.7	115°	3.5	1.8

* Specimen incomplete; ‡ shoulder overlapped. Abbreviations decypted in Introduction.

very angulate on some specimens but rounded on others. The spire height varies from nearly flat (Figures 27–29, 33) to conical (Figures 30–32). Additionally, on some specimens an abrupt enlargement of the whorl makes a bulge near the aperture (Figures 34, 36, 37).

ANDERSON (1958:168) claimed that the species occurs in considerable numbers near the Yolo-Napa County line at Putah Creek, but a search of the University of California, Berkeley, Museum of Paleontology and the California Academy of Sciences collections for specimens from that vicinity turned up only two specimens of the species from one locality, CASG loc. 2360, "Devils Gate," on Berryessa Creek, 12,000 ft (3700 m) below the top of the Chico group, on Hamilton Ranch "near the top of the big conglomerate." Anderson said that his specimens were collected from conglomerates, suggesting that *Praesargana condoni* occurs in the Venado Formation.

Superfamily BUCCINACEA Rafinesque, 1815

Family PERISSITYIDAE Popenoe & Saul, 1987

Genus *Cydas* Saul & Popenoe, gen. nov.

Type species: *Volutoderma crossi* Anderson, 1958, from the West Coast Turonian.

Diagnosis: Medium-sized, fusiform perissityids with a sloping shoulder, broadly rounded periphery, and short anterior siphonal neck that has near its anterior end a well-developed siphonal fasciole. Whorls ornamented by rounded axial ribs on posterior half of whorls over-ridden by flat-topped spiral cords. Outer lip expanded to form a rim and having a posterior, four medial, and an anterior denticle within, the central two medial denticles stronger; lip notched posteriorly at the shoulder between posterior and adapical medial denticles. Aperture elongate, narrow, sharply angled and constricted posteriorly. Parietal lip narrow and thin with one or two posterior denticles coinciding with spiral cords, two pseudofolds on columella just anterior to base of whorl; inner lip broader and thicker on columella, wrapped over to form a pseudoumbilicus anterior to fasciole.

Discussion: *Cydas* displays a typical perissityid pattern of apertural denticles. It is most similar to *Pseudocymia* Popenoe & Saul, 1987, but in *Cydas* the outer lip denticles are separated into three groups and the middle two of the medial group are the strongest, the shoulder is obscure, and the spiral cords are straplike. The posterior notch at the shoulder of the outer lip is suggestive of *Columbellaria* Rolle, 1861, but the notch is less well developed in *Cydas* and the inner lip is not expanded onto the last whorl.

The genus is named for Cydas of Gortyna, son of Antitalces, and is of masculine gender.

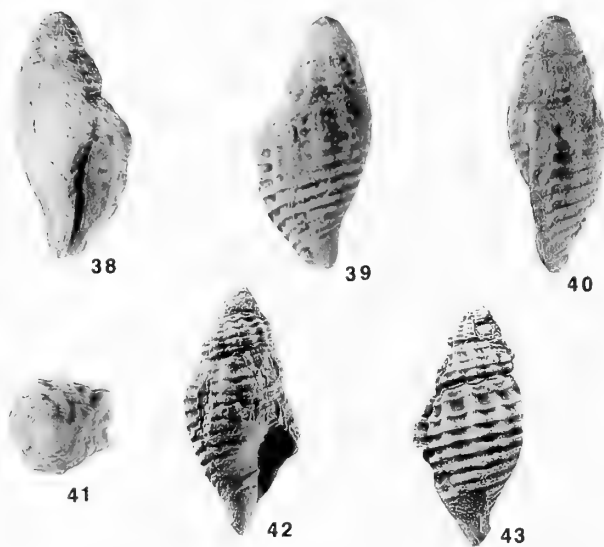
Cydas crossi (Anderson, 1958)

(Figures 38–43)

Volutoderma crossi ANDERSON, 1958:174, pl. 16, figs. 3, 3a.

Diagnosis: As for the genus.

Description: Shell of medium size, rounded fusiform; spire and last whorl of approximately equal height; apical angle about 35°; spire with five, moderately convex whorls slightly concave just below suture; body whorl ornamented with about 12 straplike spiral cords separated by interspaces as



Explanation of Figures 38 to 43

All figures $\times 1$; all specimens coated with ammonium chloride.

Figures 38–43. *Cydas crossi* (Anderson, 1958). Figures 38–40: CAS cat. no. 61934.01 from CAS loc. 61934, holotype; Figure 38, aperture; Figure 39, back; Figure 40, right side. Figures 41–43: LACMIP cat. no. 11547 from LACMIP loc. 10735, hypotype; Figure 41, apical view; Figure 42, apertural view showing pseudofold on columella; Figure 43, back. Photographs 38–41 by De Leon; 42, 43 by Susuki.

Table 5
Measurements (mm) of *Cydas crossi* (Anderson, 1958).

	H	D	Hp	Dp	Ha	A	La	Dp/Hp
CAS 61934.01	34.2*	13.9	7.0	10.8	13.6*	33°	21	1.5
LACMIP 11547	33.0*	15.5	7.4	11.5	15.5	38°	—	1.5

* Specimen incomplete. Abbreviations decrypted in Introduction.

wide as spirals, posterior spiral separated from posterior suture and succeeding abapical spiral by interspace twice its width; axial sculpture of about 12 low, rounded ribs and a varix per whorl; ribs gently arched and slightly concave to the aperture; varices, not well preserved in available specimens but developed at radial intervals of about 300°; aperture elongate, sharply angled posteriorly, contracted anteriorly; inner lip narrow, thin parietally, thicker and wider on columella, bearing one or two denticles near posterior end, and two short, slightly oblique columellar pseudofolds just anterior to whorl base; anterior tip of columella flexed slightly to the left, bearing a fasciole near its tip; outer lip expanded into a rim, bearing within a posterior, four medial, and an anterior denticle; two central medial denticles stronger; lip notched posteriorly at shoulder; labral profile nearly paralleling shell axis, but with a broad and shallow sinus concave toward the aperture.

Holotype: CASG cat. no. 61934.01 (= CASG 10675).

Hypotype: LACMIP cat. no. 11547 from LACMIP loc. 10735 (= CIT 1212), Little Cow Creek, 2 miles (3.2 km) northeast of Frazier Corners, Shasta Co., California.

Dimensions: See Table 5.

Type locality: CASG loc. 61934 (= CASG 1293D), "SW ¼ sec. 4, T32N, R3W, Frazier Corners, Shasta Co." (ANDERSON, 1958).

Distribution: Known only from the Frazier Siltstone Member of the Redding Formation in the vicinity of the type locality.

Geologic age: Late Turonian, associated with *Subprionocyclus* sp.

Remarks: Only two specimens of this species are available. Neither is complete; both lack an adequately preserved protoconch. The holotype is weathered; its shell surface is eroded, and the shell was riddled by endobionts, but the shell surface of the less complete hypotype is well preserved. The aperture of the holotype is complete enough to display a perissityid denticle pattern. The posterior "siphonal" notch is shallow, but its placement on the shoulder resembles the placement of the siphon in the Columbelloidea. Some of the early volutes, as for example the species herein assigned to *Carota*, also have an outer lip notch at the shoulder.

Cydas crossi resembles *Pseudocymia aurora* Popenoe & Saul, 1987, but *C. crossi* is more slender, has a less angulate

shoulder, fewer denticles within the outer lip, and the denticles are more clearly divided into posterior, medial, and anterior groups. *Cydas crossi* resembles *Murphitys michaeli* Saul, 1987, in overall shape but is higher spired, more slender, has spiral cords that are more straplike and regular, and has two short pseudofolds on its columella rather than the two folds of *Murphitys*.

In shape and sculptural components, *Cydas crossi* resembles the type species of *Trachytriton* Meek, 1864, *Trachytriton vinculum* (Hall & Meek, 1856), from the late Campanian-early Maastrichtian of Colorado, Montana, South Dakota, and Wyoming. *Cydas crossi* differs from *T. vinculum* in having a perissityid-like distribution of denticles within the aperture, stronger spiral sculpture consisting of fewer more nearly equal, straplike spiral cords, about half the number of axial ribs, and more irregularly developed varices, both as to strength and frequency.

Family BUCCINIDAE Rafinesque, 1815

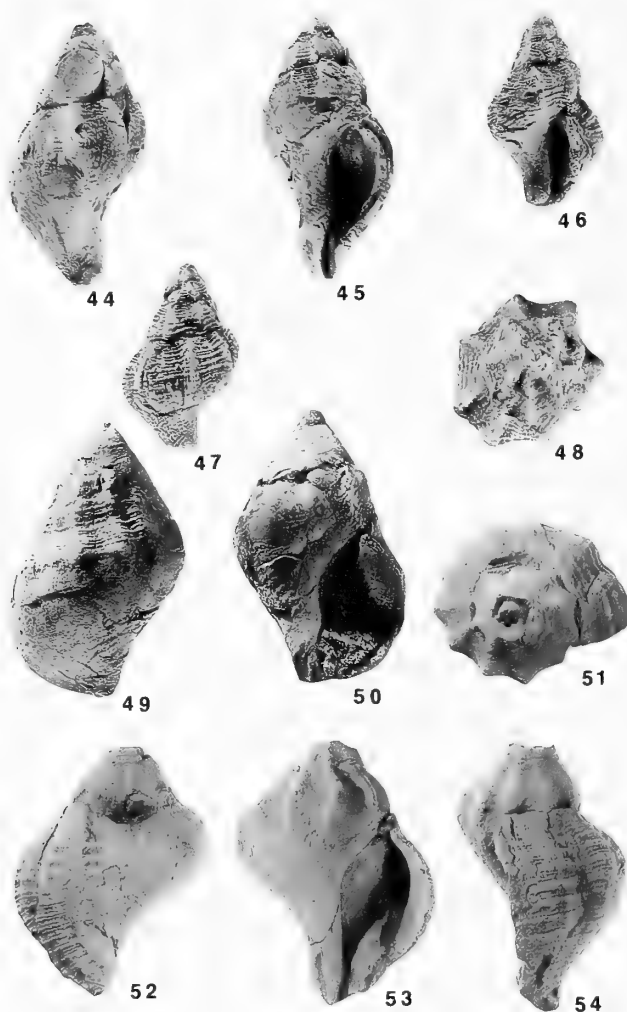
Genus *Eripachya* Gabb, 1869

Type species: *Neptunea ponderosa* Gabb, 1864, subsequent designation Cossmann, 1901, from the Campanian of California.

Diagnosis: Medium-sized, broadly fusiform buccinids having plumply convex whorls; suture sinuous, impressed. Spiral ornamentation of alternate width ribs; collabral sculpture of strong, nearly straight ribs strongest at periphery and dying out before the suture and the siphonal neck. Aperture eye-shaped, rounded posteriorly, attenuated and gently twisted anteriorly; siphonal canal narrow, moderately long; columella strongly twisted; siphonal neck bearing a narrow false umbilicus bounded by a low but well-marked fasciole; inner lip smooth, overlain by thin callus, concave in its parietal portion, gently sinuous in its columellar position; outer lip thin, lirate within.

Range: Turonian to Campanian.

Discussion: *Eripachya* has long been misunderstood. COSSMANN (1901) indicated that it was poorly characterized because the specimens were not well preserved, and he doubted that the other two species included by GABB (1869) in *Eripachya*, *Neptunea perforata* Gabb, 1864, and *Neptunea hoffmanni* Gabb, 1864, were congeneric. STEWART (1927) placed these latter species in the cancellariid genus *Paladmete* Gardner, 1916, but ANDERSON (1958) referred them back to *Eripachya* which they do not resemble. The specimen of the type species, *E. ponderosa*, figured



Explanation of Figures 44 to 54

Unless otherwise indicated, figures are $\times 1$; all specimens coated with ammonium chloride.

Figures 44–48. *Eripachya vaccina* sp. nov. Figures 44, 45: LACMIP cat. no. 11548, from LACMIP loc. 10760, holotype; Figure 44, back; Figure 45, aperture.

Figures 46–48: LACMIP cat. no. 11549, from LACMIP loc. 10776, paratype; Figure 46, aperture; Figure 47, back; Figure 48, apical view, $\times 1.5$.

Figures 49–54. *Eripachya ponderosa* (Gabb, 1964). Figures 49, 50, ANSP cat. no. 4186 from Tuscan Springs, Tehama Co., Calif., lectotype; Figure 49, back; Figure 50, aperture. Figures 51–54: CAS cat. no. 53344.01 from CAS loc. 53344, hypotype; Figure 51, apical view; Figure 52, back view; Figure 53, aperture; Figure 54, right side. Photographs 44–47, 49, 50 by Susuki; 48, 51–54 by De Leon.

by STEWART (1927:pl. 20, fig. 9) is somewhat crushed into a less bucciniform shape. *Eripachya* resembles the late Cenozoic *Lirabuccinum* Vermeij, 1991, but *Lirabuccinum* has a shorter and straighter columella, more numerous collabral ribs, and its spiral ribbing is relatively even. The

spiral sculpture of *Eripachya* has a graded or bundled aspect with wider riblets grouped together, grading into finer interspace riblets somewhat like that of *Kelletia kelletii* (Forbes, 1852).

Eripachya vaccina Saul & Popenoe, sp. nov.

(Figures 44–48)

Diagnosis: A slender *Eripachya* with about eight collabral ribs per whorl.

Description: Shell of medium size, robust, broadly fusi-form, pleural angle of about 49° ; spire approximately three-fifths the total height of the shell, with about six plumply convex whorls about twice as wide as high; siphonal neck slightly longer than the spire with a well-marked fasciole; suture undulating, slightly appressed. Protoconch unknown. Sculpture of fine spiral cords and strong collabral ribs; spiral ornamentation of five or six low, flat, narrow primary cords on penultimate whorl, and about 15 on body whorl and neck, separated by interspaces wider than the primaries, and alternating with narrow threadlike secondary spirals; seven or eight sharp-crested collabral ribs per whorl separated by flatish interspaces, twice the width of the ribs; ribs on body whorl diminishing anterior to the periphery, not present on base or siphonal neck, disappearing at about the mid-length of whorl. Aperture eye-shaped, angulate at the suture, broad posteriorly, attenuated anteriorly; siphonal canal narrow, of moderate length, twisted abaperturally and to the left anteriorly, bearing above its tip a narrow and shallow umbilical chink bounded by a low but well-marked fasciole; inner lip smooth, without folds, parietal lip short, columellar portion nearly straight, bent at the fasciole and with a free edge forming a pseudoumbilicus with the fasciole; outer lip unknown.

Holotype: LACMIP cat. no. 11548.

Paratype: LACMIP cat. no. 11549 from LACMIP loc. 10776 (= CIT loc. 1197), Stinking Creek, Shasta Co., California.

Type locality: LACMIP loc. 10760 (= CIT loc. 1438), north side Little Cow Creek, Shasta Co., California.

Dimensions: See Table 6.

Geologic age: ?Early Turonian, horizon of *Tragodesmoceras*.

Distribution: Redding Formation, Bellavista Sandstone Member of the Redding area, Shasta Co., California.

Remarks: *Eripachya vaccina* is a rare form; only two incomplete specimens are in the LACMIP collection. Both specimens lack a protoconch, the outer lip, and the parietal portion of the inner lip. *Eripachya vaccina* is more slender, has a longer anterior siphonal canal, and is ornamented with fewer secondary spirals than the type species, *E. ponderosa*. The holotype of *E. vaccina* shows no lirae on the outer lip but is broken back too far to be sure that lirae

were not present. Additionally the shape of the parietal portion of the inner lip is undeterminable, as is the presence of a posterior siphonal notch at the suture.

Etymology: The specific name *vaccina*, Latin, meaning of cows, refers to the type locality on the north side of Little Cow Creek.

Eripachya ponderosa (Gabb, 1864)

(Figures 49–54)

Neptunea ponderosa GABB, 1864:88, pl. 18, fig. 38.

Eripachya ponderosa (Gabb): GABB, 1869:149; COSSMANN, 1901:147, fig. 40; STEWART, 1927:425, pl. 20, fig. 9; WENZ, 1941:1185, fig. 3373; ANDERSON, 1958:172.

Description: Shell of medium size, robust, bucciniform, apical angle of about 80°; spire approximately two-thirds the total height of the shell, with about six plumply convex whorls about twice as wide as high; suture undulating, and appressed; siphonal neck broad, barely longer than the spire, with a low well-developed fasciole. Sculpture of narrow spiral cords and strong collabral ribs; five or six primary spiral cords on penultimate whorl, 15 on body whorl and neck, low, flat, narrow, each bordered by graded sets of finer ribs; ten, moderately sharp-crested collabral ribs on early whorls, becoming broader, well rounded on body whorl, about as wide as interspaces, diminishing anteriorly to the periphery, disappearing on base of whorl. Aperture eye-shaped, broad posteriorly with a small narrow posterior channel at the suture, attenuated anteriorly; siphonal canal moderately narrow, short, tip flexed backward and to left; inner lip smooth, without folds, parietal portion thin, rounded; columellar portion thicker, nearly straight, with a free edge forming a narrow, shallow umbilical chink anterior to the fasciole; outer lip thin, lirate within.

Lectotype: ANSP cat. no. 4186, here designated.

Hypotype: CASG cat. no. 53344.01 (= CSMB cat. no. 12793) from Tuscan Springs, Tehama Co., California.

Dimensions: See Table 6.

Type locality: Tuscan Springs, on Little Salt Creek, Tehama Co., California.

Distribution: A rare species, known predominantly from the type locality. Some small poorly preserved specimens from the Schultz Member of the Williams Formation in the Santa Ana Mountains (UCLA loc. 7199), Orange Co., may be this species.

Geologic age: Campanian.

Remarks: STEWART (1927) figured ANSP cat. no. 4186 and referred to it as the holotype because he considered it to be the specimen GABB (1864) had figured. Gabb, however, did not designate type specimens, and he mentions more than one specimen, but other specimens in the box

Table 6

Measurements (mm) of *Eripachya vaccina* sp. nov. and *E. ponderosa* (Gabb, 1864).

	H	D	Hp	Dp	Ha	A	R	Dp/ Hp
<i>E. vaccina</i>								
LACMIP								
11548	33.0*	17.5	6.4	11.7	12.0*	49°	8	1.8
LACMIP								
11549	24.7*	14.3	5.5	9.0	12.8	46°	8	1.6
<i>E. ponderosa</i>								
CAS 5334401	36.0*	28.7	9.0	14.6	12.0*	77°	11	1.6
UCLA								
28733**	34.6	23.2†	9.6	12.8	13.5	60°†	11	1.3

* Specimen incomplete; † specimen crushed; ** plastercast of ANSP 4186. Abbreviations decrypted in Introduction.

with Stewart's figured specimen were "*Fulgur*" *hilgardi* White, 1889. Gabb did not differentiate "*Fulgur*" *hilgardi* from *Eripachya ponderosa*, and his specimens of *E. ponderosa* from Pentz are apparently "*F.*" *hilgardi*. As STEWART (1927) did in several instances designate lectotypes, his reference to ANSP 4186 as holotype is an error and cannot be taken as designation of the lectotype. To avoid possible confusion, Stewart's figured specimen ANSP 4186 is therefore herein designated the lectotype.

Eripachya ponderosa differs from *E. vaccina* in being stouter, having a shorter anterior canal, and having one more secondary spiral thread in each interspace.

Eripachya ponderosa of DAILEY & POPENOE (1966) is early Maastrichtian in age, lacks axial sculpture, and is an undescribed species.

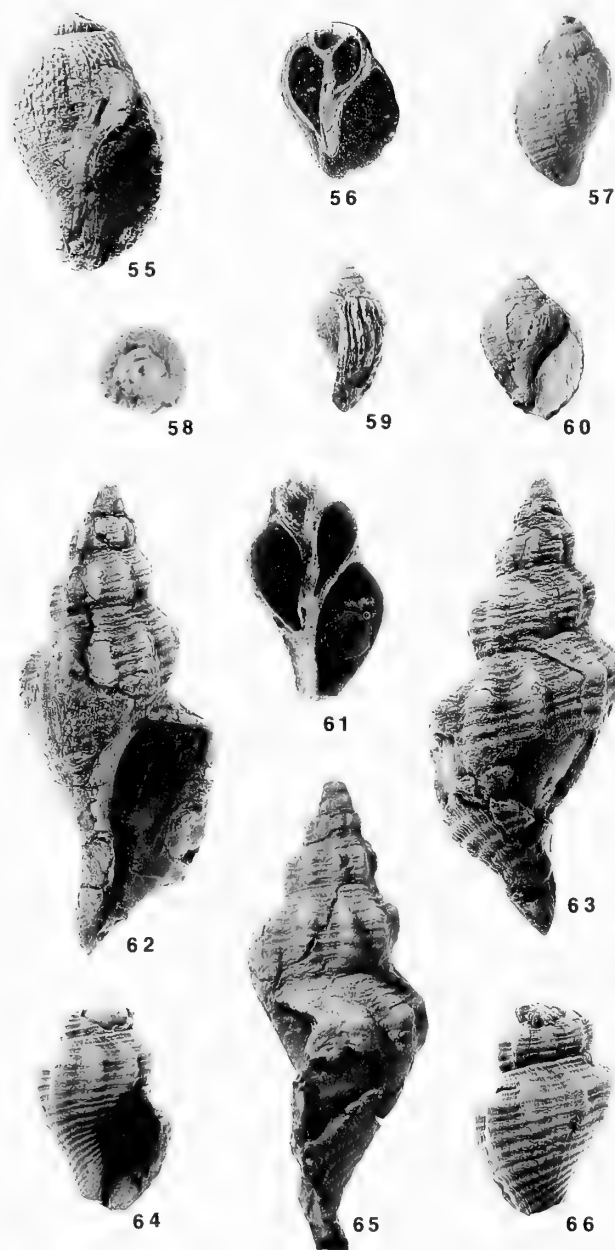
Family MELONGENIDAE Gill, 1871

Genus *Palaeatractus* Gabb, 1869

Type species: By monotypy, *Palaeatractus crassus* Gabb, 1869 from the Turonian of California.

Diagnosis: Small, thick-shelled, pyriform, ornately sculptured melongenids with a slightly twisted columella, simple outer lip, and thick inner lip.

Discussion: These are small shells, considerably smaller than such forms as *Pyrifusus* Conrad, 1858, or *Sycostoma* Cox, 1931, with which WENZ (1941) has associated *Palaeatractus*. The genus is, however, similar in overall shape to these larger forms but has stronger sculpture and a more bent canal than *Sycostoma*, and lacks the subsutural welt and concave band of *Pyrifusus*. The sculpture and shape of *Palaeatractus* recall that of the pseudolivine *Pegocomptus* Zinsmeister, 1983, and the volute *Volutocorbis* (*Retipirula*) *crassatesta* (Gabb, 1869) (ZINSMEISTER, 1977), but *Palaeatractus* has no pseudolivine groove on the body whorl, no folds on the columella, and has finer sculpture.



Explanation of Figures 55 to 66

Unless otherwise indicated, figures are $\times 1$; specimens coated with ammonium chloride, except as noted.

Figures 55–60. *Palaeatractus crassus* Gabb, 1869. Figure 55: LACMIP cat. no. 11550, from LACMIP loc. 10744, neotype, aperture, $\times 3$. Figure 56: LACMIP cat. no. 11552, from LACMIP loc. 10744, hypotype, section showing lack of folds on columella, $\times 3$, uncoated. Figures 57, 58: LACMIP cat. no. 11551, from LACMIP loc. 10744, hypotype; Figure 57, back, $\times 3$; Figure 58, apical view, $\times 3$. Figures 59, 60: LACMIP cat. no. 11553, from UCLA loc. 4214, hypotype; Figure 59, right side; Figure 60, aperture.

Figures 61–66. *Saturnus dubius* (Packard, 1922). Figure 61: LACMIP cat. no. 11556, from LACMIP loc. 10079, section showing lack of folds on columella, hypotype, uncoated.

Table 7

Measurements (mm) of *Palaeatractus crassus* (Gabb, 1869).

	H	D	Hp	Dp	Ha	A	Dp/ Hp
LACMIP 11550	10.9*	6.5	1.9	3.5	2.3*	68°	1.8
LACMIP 11551	7.8	4.4	1.4	2.6	2.5	66°	1.9
LACMIP 11552	6.5	4.9	—	—	—	—	—
LACMIP 11553	20.0*	19.6	2.8	5.6	4.7	86°	2.0

* Specimen incomplete. Abbreviations decypted in Introduction.

Palaeatractus crassus Gabb, 1869

(Figures 55–60)

Palaeatractus crassus GABB, 1869:148, pl. 26, fig. 26;
COSSMANN, 1901:82, text fig. 24; WENZ, 1941:1222, fig. 3476.

Diagnosis: Small pyriform shells with a low spire, thick shell, slightly twisted columella, simple outer lip, incrustated inner lip, and a strong, overall sculpture of squarish nodes.

Description: Shell small, pyriform, thick; spire low; whorls five, rounded; suture impressed. Surface marked by prominent, straplike spiral ribbons, crossed by irregular axial ribs or lines; axial ribs variable in size, number, and disposition, but generally of nearly even distribution, producing squarish nodes or tubercles at intersections with spiral ribbons; interspaces showing numerous fine growth lines. Aperture broad in middle, acute posteriorly, extended anteriorly into moderate and slightly twisted canal; outer lip simple; inner lip thick, expanded roundly onto body whorl, extending adapically beyond aperture, with a well defined margin; columella without folds.

Neotype: LACMIP cat. no. 11550. STEWART (1927) was unable to find Gabb's specimens of this species. In their absence, a neotype is herein chosen from LACMIP loc. 10744 (= CIT 1255).

Hypotypes: LACMIP cat. nos. 11551–11552 from LACMIP loc. 10744 (= CIT loc. 1255), French Creek, north of Swede Basin; 11553 from UCLA loc. 4214, Little Cow Creek, Shasta Co., California.

Dimensions: See Table 7.

Original type locality: From the Shasta Group, from a canyon in the foothills, a mile (1.6 km) south of the road from Colusa to the Sulphur Springs near the eastern margin of the Coast Range, Colusa County, California.

Figures 62, 63, 65: LACMIP cat. no. 11554, from LACMIP loc. 10079, hypotype; Figure 62, aperture; Figure 63, back; Figure 65, right side. Figures 64, 66: LACMIP cat. no. 11555, from LACMIP loc. 10079, hypotype; Figure 64, aperture; Figure 66, back. Photographs 55, 56, 61–64 by Susuki; 57–60, 65 by De Leon.

Locality of the neotype: LACMIP loc. 10744, French Creek, north of Swede Basin, Shasta Co., California.

Distribution: Redding Formation, Frazier Siltstone Member and near the base of the Melton Sandstone Member, Swede Creek Valley, Redding area, Shasta Co.; Great Valley Series, Colusa Co., California. ANDERSON (1958: 26) listed this species from the second conglomerate above the base of the Pacheco Group on Bear Creek, Colusa Co., but the specimens have not been found at either the California Academy of Sciences or the University of California, Berkeley, Museum of Paleontology.

Geologic age: Turonian.

Remarks: The sculpture of squarish, flat nodes is distinctive. Weathering causes the nodes to become pitted and produces a more ornate, pseudocancellate effect (Figure 55).

Although GABB (1869) indicated that his lot of fossils from south of the road from Colusa to the Sulphur Springs, Colusa County was from the Shasta Group, which is of Early Cretaceous age, this species has not been found associated with others of Early Cretaceous age and is present in beds of Turonian age in the Redding area. ANDERSON (1938:131) interpreted Gabb's locality to be in the first range of foothills on the west side of the Sacramento Valley and south of the road between Colusa and Wilber Springs. He referred this locality to the younger "Chico" beds rather than the older "Shasta" strata. We have not seen any collection that might be from this vicinity, and there is no record of any such collection in the literature. The possibility that a collector might stumble upon this locality and provide topotype or near topotype specimens cannot be ruled out, but the probability that the Redding area specimens are correctly determined is very large. The selection of this neotype provides additional characteristics for recognizing the genus and the species, and for classifying the genus.

COSSMANN (1901) referred three species to *Palaeatractus*: *P. minimus* (Hoeninghaus in Goldfuss, 1844) and *P. roemeri* Holzapfel, 1888, from Vaals, Netherlands, "near Aix-la-Chapelle" = Aachen; and "*Voluta*" *rhomboidalis* Zekeli, 1852, from Gosau, Austria. ZEKELI's (1852) figure of "*V.*" *rhomboidalis* (pl. 14, fig. 9) has a more angular whorl profile, less twist to the anterior canal, and lacks the expanded, thickened inner lip of *P. crassus*. STOLICZKA's (1867: 120, pl. 10, fig. 21, 21a) "*V.*" *rhomboidalis* from the Arrialoor Group (Campanian-Maastrichtian) of southern India has a more rounded whorl profile similar to that of *P. crassus*, and may not be Zekeli's species. The Indian form also does not show the expanded demarked inner lip of *P. crassus*, and Stoliczka suggested that in "*V.*" *rhomboidalis* the sculpture diminishes with maturity, which is not true for *P. crassus*. None of these is a convincing *Palaeatractus*.

GABB (1869:148) gave the dimensions of his figured specimen as "Length .62 inch [=16 mm]; width .45 inch [=11.43 mm]; length of aperture .5 inch" [=12.7 mm]; but

he drew a size bar (GABB, 1869:pl. 26, fig. 26) 0.8 inch (=20.32 mm) long. WENZ (1941:1223, Abb. 3476) reprinted Gabb's figure, which is 39 mm (=1.5 inches) high, and more than twice Gabb's described height but less than two times his diagrammed height, as being 1/1. Three of the four specimens from Swede Basin in the Redding area are small (6.5 to 10.9 mm high) and close to the height(s) indicated by GABB (1869), but one is larger (20.0 mm high). This specimen, although incomplete and larger than Gabb's size bar, is considerably smaller than Gabb's (or Wenz') figure. Size range of the Redding specimens is probably representative of the species.

The specimen from CASG loc. 1552, north end of the Shale Hills in Antelope Valley, Kern Co., California, identified by ANDERSON (1958:58) as *Palaeatractus crassus* is not this species, but is instead a volute resembling *Konistra biconica* (ANDERSON, 1958). Although ANDERSON (1958) suggested that these beds were of Coniacian age, MATSUMOTO (1960:80) indicated that they are late Campanian-early Maastrichtian in age.

Saturnus Saul & Popenoe, gen. nov.

Type species: *Siphonalia dubius* Packard, 1922, from the Turonian of Southern California.

Diagnosis: Shell fusiform, spire fairly high; whorls angularly shouldered posteriorly with a moderate ramp. Growth lines prosocline at suture, strongly sinused at shoulder, and broadly arcuate across flank. Sculpture of spiral ribbons over riding collabral ribs; collabral ribs strong, rounded, accentuated by nodes at shoulder, dying out above and below. Aperture notched posteriorly at shoulder, siphonal canal curved to left; outer lip smooth; columella smooth; inner lip well marked and forming a narrow pseudumbilicus at fasciole.

Discussion: *Saturnus* resembles *Deussenia* Stephenson, 1941, from the Late Cretaceous of the Gulf Coast, but lacks a subsutural collar, having only a subsutural welt. The posterior end of the aperture makes a broad angle rather than a narrow channel as in *Deussenia*. Although the notch in the growth line at the shoulder is suggestive of a turrid, and *Saturnus* bears some resemblance to *Knefastia* Dall, 1919, the shoulder notch of *Saturnus* is shallow and its growth line is similar to that of melongenids.

The genus is named for the Roman god of agriculture, *Saturnus*, and is of masculine gender.

Saturnus dubius (Packard, 1922)

(Figures 61–66)

Siphonalia dubia PACKARD, 1922:431, pl. 35, fig. 5.

Diagnosis: As for the genus.

Description: Medium-sized fusiform shells with a spire about one-third total shell height; pleural angle about 47°; protoconch unknown; suture appressed with a slight subsutural welt; body constricted posteriorly to form a shallow

Table 8
Measurements (mm) of *Saturnus dubius* (Packard, 1922).

	H	D	Hp	Dp	Ha	Hs	A	R	Dp/Hp	Hp/Hs
LACMIP 11554	62.8	25.8	12.3	17.8	21.0	8.5	47°	10	1.4	1.4
LACMIP 11555	27.5*	14.8	7.6	13.7	—	4.9	44°	9	1.8	1.6
LACMIP 11556	30.4*	20.7	—	—	—	—	46°	—	—	—

* Specimen incomplete. Abbreviations decrypted in Introduction.

ramp, slightly swollen below nodose shoulder, and tapering anteriorly. Sculpture of strong, broad, rounded collabral ribs, about 10 per whorl, arising at shoulder and dying out on flank, all overridden by flat-topped spiral ribbons narrower than interspaces, four or five ribbons on whorl flanks of spire, at least 12 on body whorl flank, and about six on ramp. Growth lines prosocline at suture, becoming strongly opisthocline on ramp, sinused at shoulder, becoming orthocline over periphery and base. Aperture rather ear-shaped with a broad posterior notch and a stronger notch at shoulder; anterior canal elongate, slightly twisted, and inclined to the left; inner lip moderately thick, well demarked, rounded parietally, forming an elongate chink-like pseudoumbilicus along fasciole.

Holotype: UCBMP cat. no. 12304.

Hypotypes: LACMIP cat. no. 11554–11556 from LACMIP loc. 10079 (= CIT loc. 1164), south side Silverado Canyon, Santa Ana Mts., Orange Co., California.

Type locality: “from the Chico of the Santa Ana Mountains, Orange Co., California” (Packard, 1922).

Dimensions: See Table 8.

Geologic age: Turonian.

Distribution: Known from several localities, all near the top of the Baker Canyon Member or the base of the overlying Holz Shale Member, Ladd Formation, Santa Ana Mountains, Orange Co., California.

Remarks: PACKARD's (1922:431) specimen was imprecisely located, and he was unable to determine the horizon of this species. It resembles *Deussenia ripleyana* Harbison, 1945, from the Ripley Formation of the Gulf Coast but is higher spired, has stronger and fewer collabral ribs, and a fasciole with a very narrow pseudoumbilicus. The aperture has a broader posterior notch and a stronger, wider shoulder notch.

Family FASCIOLARIIDAE Gray, 1853

Subfamily FASCIOLARIINAE Gray, 1853

Genus *Drilluta* Wade, 1916

Type species: *Drilluta communis* Wade, 1916, by original designation, from the Maastrichtian of Tennessee.

Diagnosis: Rather slender fusiform shells with a spire about half total shell height. Whorls posteriorly constricted

to a roughened subsutural collar. Sculpture usually dominated by strong collabral transverse ribs; spiral sculpture well developed on basal slope, less frequently on periphery. Aperture notched posteriorly, siphonal canal of moderate length and slightly inclined to left. Inner lip callus thin; columella with a strong plait anterior to one or two weaker folds (SOHL, 1964:205).

Discussion: WADE (1916), STEPHENSON (1941), and PILSBRY & OLSSON (1954) considered *Drilluta* to belong to the Volutidae, but WENZ (1943:1418) placed it in the Conacea. SOHL (1964:205) considers it close to *Bellifusus* Stephenson, 1941 (type species *Odontofusus curvicostata* Wade, 1926, Maastrichtian, Gulf Coast), and places it in the Fasciolariidae.

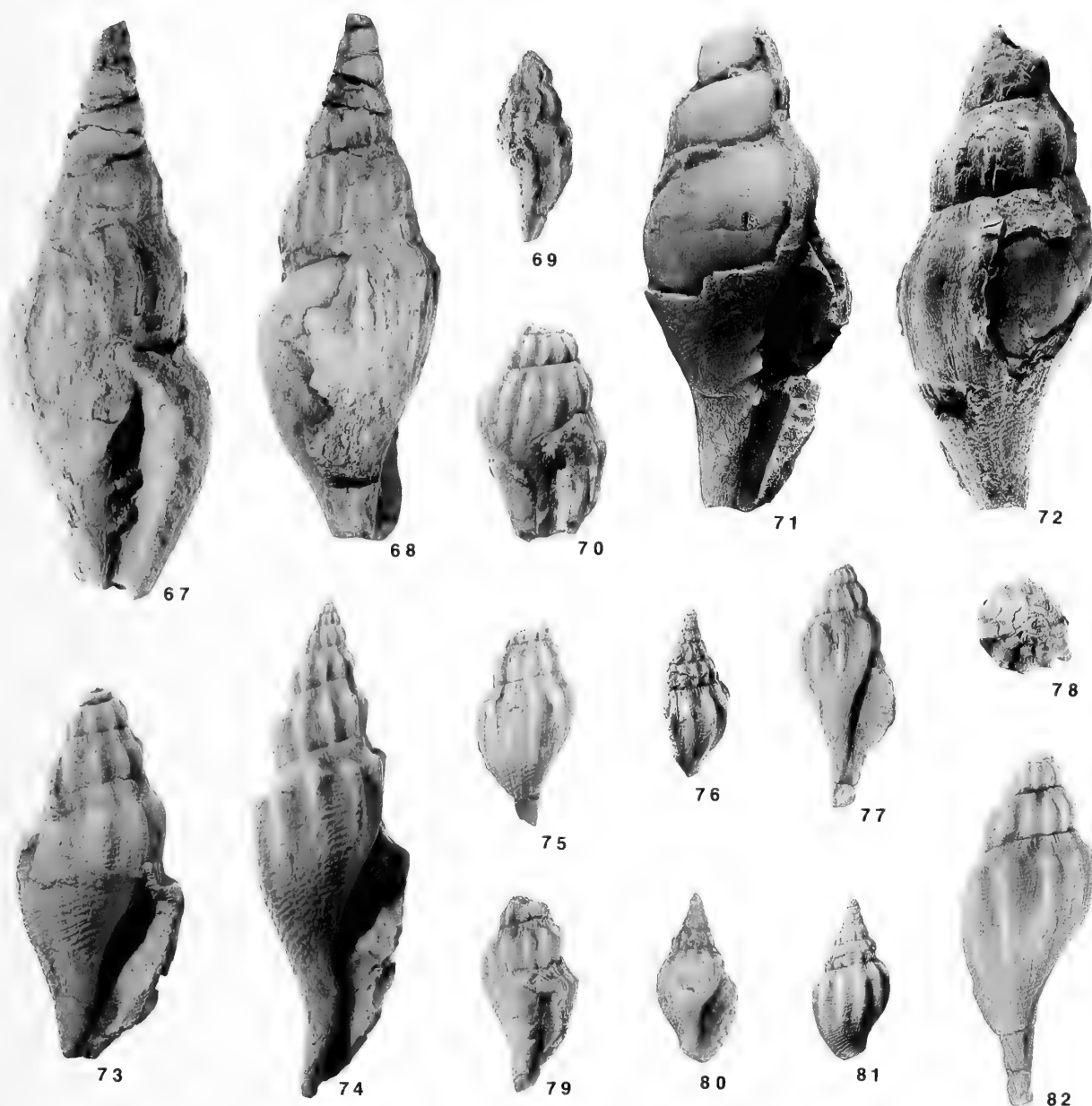
Drilluta jacksonensis (Anderson, 1958)

(Figures 67–72)

Volutoderma? *jacksonensis* ANDERSON, 1958:174, pl. 21, fig. 1.

Diagnosis: A large *Drilluta* with a weakly developed subsutural collar, moderately strong shoulder, elongate body whorl, 13 to 18 wide-spaced strong, sigmoidal collabral ribs, and faint spiral sculpture on base of body whorl and siphonal neck. Shoulder at about mid whorl height on spire.

Description: Shell large, elongate fusiform, apical angle about 33°; spire broken but probably approximately of same length as body whorl; whorls of spire about one-third broader than high, with a steeply sloping, moderately broad and very shallowly concave ramp to noded shoulder, shoulder at about mid whorl height, flanks slightly convex; suture sinuous, appressed, with weakly developed, wrinkled subsutural collar; body whorl with a steeply sloping concave ramp to noded shoulder, gently convex lateral areas, and concave gently tapering, moderately long siphonal portion; axial sculpture of 13 to 18 rather widely spaced, collabral ribs to the whorl; ribs concave toward aperture, most strongly developed on shoulder of whorl, diminishing and disappearing rapidly anteriorly, and usually more or less obsolete on the concave ramp; spiral sculpture of close-set, faint, revolving lines usually apparent only on base of body whorl and siphonal neck. Aperture narrow, parietal border of aperture shallowly excavated; columella of medium length, nearly straight, bearing prox-



Explanation of Figures 67 to 82

All specimens coated with ammonium chloride; unless otherwise indicated figures are $\times 1$.

Figures 67–72. *Drilluta jacksonensis* (Anderson, 1958). Figures 67, 68: CAS cat. no. 445.16 from CAS loc. 445, holotype; Figure 67, aperture; Figure 68, left side. Figure 69: LACMIP cat. no. 11584 from LACMIP loc. 10778, hypotype, aperture. Figure 70: LACMIP cat. no. 11562 from LACMIP loc. 10771, hypotype, aperture. Figures 71, 72: LACMIP cat. no. 11557 from LACMIP loc. 10750, hypotype; Figure 71, aperture; Figure 72, back.

Figures 73–82. *Drilluta sicca* sp. nov. Figure 73: CAS cat. no. 445.31 from CAS loc. 445, holotype, aperture. Figure 74: LAC-

MIP cat. no. 11563 from LACMIP loc. 10903, paratype, aperture. Figures 75, 79: LACMIP cat. no. 11566 from LACMIP loc. 10903, paratype; Figure 75, back view; Figure 79, aperture showing columellar folds.

Figures 76, 80, 81: LACMIP cat. no. 11559 from LACMIP loc. 10810, paratype; Figure 76, right side, $\times 2$; Figure 80, aperture, $\times 2$; Figure 81, back, $\times 2$. Figures 77, 78, 82: LACMIP cat. no. 11565 from LACMIP loc. 10769, paratype; Figure 77, aperture; Figure 78, apical view; Figure 82, left side, $\times 1.5$. Photographs 67–70, 73–82 by De Leon; 71, 72 by Susuki.

Table 9
Measurements (mm) of *Drilluta jacksonensis* (Anderson, 1958) and *D. sicca* sp. nov.

	H	D	Hp	Dp	Ha	Hs	A	R	Dp/Hp	Hp/Hs
<i>D. jacksonensis</i>										
CAS 445.16	85.0*	33.9	16.2	23.8	47.0*	8.7	33°	17	1.5	1.9
LACMIP 11557	70.6*	30.0	14.4	23.0	27.9*	7.0	35°	14	1.6	2.1
LACMIP 11558	32.0*	14.8†	7.6	10.8†	—	4.0	32°†	13	1.4	1.9
LACMIP 11562	32.0*	15.0†	7.8	10.0	—	4.0	40°†	14	1.3	2.0
LACMIP 11584	27.8*	11.5	5.0	7.8	11.4	2.7	41°	13	1.6	1.8
<i>D. sicca</i>										
CAS 445.31	56.5*	26.3†	12.8	18.6	25.6	8.9	37°	10	1.4	1.4
LACMIP 11559	12.8*	6.1	1.9	4.0	6.5	1.5	43°	12	2.1	1.3
LACMIP 11560	11.4*	5.6	2.0	—	—	1.2	—	11	—	1.7
LACMIP 11561●	—	—	—	—	—	—	39°	12	—	—
LACMIP 11563	70.0	22.3	11.7	16.0	31.0	9.0	32°	10	1.4	1.3
LACMIP 11564●	54.7*	—	8.4	—	—	5.5	—	—	—	1.5
LACMIP 11565	34.7*	16.0	7.0	11.0	12.5	4.5	41°	11	1.6	1.6
LACMIP 11566	29.2*	14.7	7.5	13.0	—	4.7	38°	12	1.7	1.6
UW 91830	33.7*	13.7	6.5	10.5	14.3	4.5	45°	12	1.6	1.4

* Specimen incomplete; † specimen crushed; ● latex pull. Abbreviations decrypted in Introduction.

imally three oblique prominent revolving folds, anterior fold strongest; no basal fasciole.

Holotype: CASG cat. no. 445.16.

Hypotypes: LACMIP cat. nos. 11557 from LACMIP loc. 10750 (= CIT loc. 1264); 11562 from LACMIP loc. 10771 (= CIT loc. 1209), Salt Creek; 11584 from LACMIP loc. 10778 (= CIT loc. 1195; UCLA loc. 4416), Stinking Creek, Shasta Co., California.

Dimensions: See Table 9.

Type locality: CASG loc. 445, Forty-nine mine, two miles (3.2 km) south of Phoenix, Jackson Co., Oregon.

Distribution: Redding Formation, Bellavista Sandstone Member, Stinking Creek, Melton Sandstone Member, Little Cow Creek area, Shasta Co., California.

Geologic age: Turonian.

Remarks: Although ANDERSON (1958) described this species as lacking spiral sculpture, faint spiral lines are present on the base of the body whorl and siphonal neck. *Drilluta jacksonensis* differs from *D. sicca* in having more and narrower collabral ribs, fainter spiral sculpture, and a weaker shoulder that is at about mid whorl on the spire. *Drilluta jacksonensis* has a more inconspicuous subsutural collar than does *D. sicca* and than have other species of *Drilluta*. Of three similar Gulf Coast genera, *Drilluta* (large, collared), *Paleopsephaea* Wade, 1926 (type species *P. mutabilis* Wade, 1926, medium sized, not collared), and *Bellifusus* (medium sized, collared), *D. jacksonensis* is most like *Drilluta* in size, shape, and columellar folds. Among Gulf Coast species of *Drilluta*, *D. jacksonensis* is most similar to *D. communis* (WADE, 1916:459, pl. 23, figs. 5–6; SOHL, 1964:

205, pl. 27, figs. 12–13, 20–22) in size and shape, but has a wider ramp and more poorly developed subsutural collar.

Drilluta sicca Saul & Popenoe, sp. nov.

(Figures 73–82)

Diagnosis: A volutiform *Drilluta* with moderately developed, wrinkled collar, slightly concave ramp, and 10–12 strongly shouldered, nearly straight collabral ribs per whorl. On spire, shoulder at about two-thirds whorl height.

Description: Shell medium sized, elongate volutiform; apical angle about 40°; spire shorter than body whorl; whorls of spire about one-third broader than high, with a sloping, moderately broad, and very shallowly concave ramp to noded shoulder; shoulder at two-thirds whorl height; flanks rather straight; suture sinuous, appressed with moderately developed, wrinkled subsutural collar; body whorl with concave ramp to noded shoulder, barely convex lateral areas, and concave, gently tapering, moderately long siphonal portion. Sculpture of 10 to 12 rather widely spaced, nearly straight, sharp collabral ribs per whorl, over-ridden by spiral riblets, weak on ramp and shoulder, stronger abapical to the mid-flank. Aperture narrow, parietal border of aperture shallowly excavated; columella bearing two oblique, moderately strong folds, anterior fold stronger, and a faint third, posterior fold; inner lip thin, of moderate width, rounded on the base of the whorl.

Holotype: CASG cat. no. 445.31.

Paratypes: LACMIP cat. nos. 11559–11561 from LACMIP loc. 10810 (= CIT loc. 1207), Dry Creek; 11563 from LACMIP loc. 10771 (= CIT loc. 1209), Salt Creek;

LACMIP cat. no. 11564 from LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek; LACMIP cat. no. 11565 from LACMIP loc. 10769 (= CIT loc. 1203), Dry Creek, Shasta Co., California; LACMIP cat. no. 11566 from LACMIP loc. 10903 (= CIT loc. 1622), south of Ashland, Jackson Co., Oregon; UW cat. no. 91830 from UW loc. B5900, Sidney Island, British Columbia.

Type locality: CASG loc. 445, Forty-nine mine, two miles (3.2 km) south of Phoenix, Jackson Co., Oregon.

Dimensions: See Table 9.

Distribution: Unnamed formation, Sidney Island (coll. Peter Ward, 3 September 1992), British Columbia; Hornbrook Formation, near Phoenix, Jackson Co., Oregon; Redding Formation, Bellavista Sandstone Member, Frazier Siltstone Member, and Melton Sandstone Member, Redding area, Shasta Co., California.

Geologic age: Turonian.

Remarks: *Drilluta sicca* resembles *D. distans* (Conrad, 1860) from the Ripley Formation of the Gulf Coast, but the West Coast form is more strongly shouldered. *Drilluta sicca* is lower spired, has a more prominent shoulder, has fewer, stronger, straighter collabral ribs, and has stronger spiral riblets than *D. jacksonensis*. *Drilluta sicca* resembles *Varens anae* sp. nov. in overall shape, but *V. anae* lacks spiral sculpture and has a broad, straight anterior canal whereas that of *D. sicca* is slender and twisted.

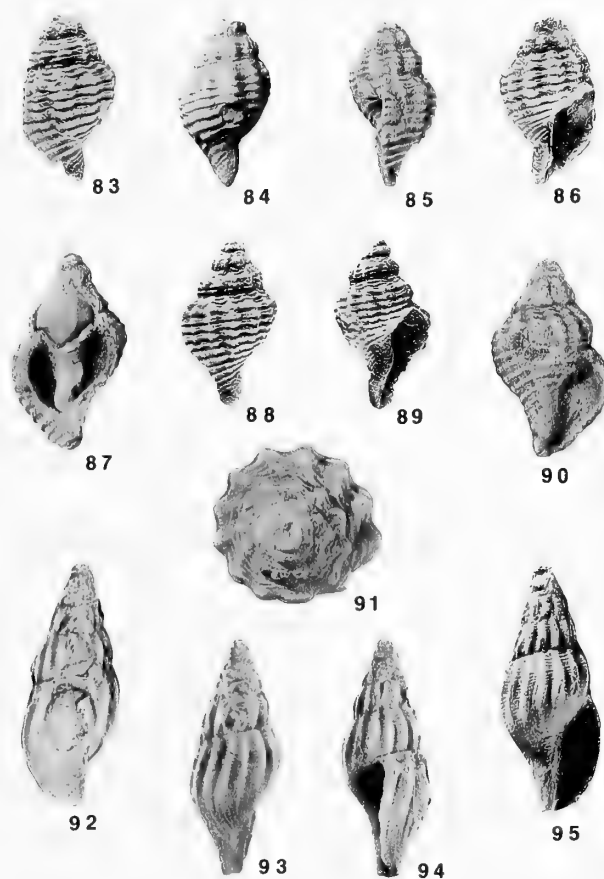
Both *Drilluta sicca* and *D. jacksonensis* are of late Turonian age at their type locality (MATSUMOTO, 1960:77), but both are also found in the slightly older Bellavista Sandstone Member of the Redding Formation.

Etymology: The specific name refers to the type locality on Dry Creek, *siccus*, Latin, meaning dry.

Genus *Skyles* Saul & Popenoe, gen. nov.

Type species: *Skyles salsus* Saul & Popenoe, sp. nov.

Diagnosis: A medium-sized, broadly fusiform fasciolarid with a moderate spire and broad apical angle; suture impressed and sinuous; last whorl longer than the spire, roundly convex from posterior suture to neck of siphonal canal, constricted basally to form siphonal neck; growth lines and labral profile gently sigmoid, antecurrent at suture, concave aperturally below suture. Sculpture of raised spiral straps and low strong, nearly straight, rounded axial ribs, well developed on posterior half of last whorl. Aperture elliptical with a short, parallel-sided, leftward-bent anterior sinus; inner lip thin, oblique and twisted to the left siphonally, bearing one oblique inconspicuous fold at juncture of canal and aperture; columella twisted to left distally; outer lip thin, transversely lirate at its edge; siphonal fasciole low, broad, enclosing a minute umbilical chink.



Explanation of Figures 83-95

Unless otherwise indicated, figures are $\times 1$; all specimens coated with ammonium chloride.

Figures 83-91. *Skyles salsus* sp. nov. Figures 83-86: LACMIP cat. no. 11568 from LACMIP loc. 10735, paratype; Figure 83, aperture; Figure 84, left side; Figure 85, right side; Figure 86, aperture. Figures 87, 90: LACMIP cat. no. 11569 from LACMIP loc. 10735, paratype; back cut away to show columellar fold; Figure 90, aperture. Figures 88, 89, 91: LACMIP cat. no. 11567 from LACMIP loc. 10735, holotype; back view; Figure 89, aperture; Figure 91, apical view, $\times 2$.

Figures 92-94. *Remera vacca* sp. nov., LACMIP cat. no. 11570 from LACMIP loc. 1446, holotype; Figure 92, back, $\times 3.5$; Figure 93, left side, $\times 3.5$; Figure 94, right side, $\times 3.5$; Figure 95, aperture, $\times 3.5$. Photographs 83, 86, 88, 89, 95 by Susuki; 84, 85, 87, 90-94 by De Leon.

Discussion: *Skyles* is similar to *Ornopsis* Wade, 1926 (type species *O. glenni* Wade, 1916, Maastrichtian, Gulf Coast), from which *Skyles* differs in having the axial ribs more persistent posteriorly, lacking a concave subsutural band, having coarser, more widely spaced spiral sculpture, and having a shorter siphonal canal. Although the columellar fold of *Skyles* is similar to that of *Ornopsis*, the absence of a concave subsutural band in *Skyles* gives it a more bucciniform whorl profile.

Table 10

Measurements (mm) of *Skyles salsus* sp. nov.

	H	D	Hp	Dp	Ha	A	R	Dp/ Hp
LACMIP								
11567	22.4*	12.0	4.0	10.0	9.3	52°	12	2.5
LACMIP								
11568	22.0	12.5	4.8	9.8	9.1	62°	11	2.0
LACMIP								
11569	26.4	16.0	6.4	11.2	13.0	60°	—	1.8

* Specimen incomplete. Abbreviations decrypted in Introduction.

The genus is named for Scyles, a Scythian king who was beheaded by his brother, and is of masculine gender.

Skyles salsus Saul & Popenoe, sp. nov.

(Figures 83–95)

Diagnosis: As for the genus.

Description: Shell medium sized, broadly fusiform; spire about two-fifths the height of the shell, apical angle 55°; whorls five, evenly convex, about twice as wide as high; suture linear, impressed, and sinuous; last whorl about half as long again as spire, broadly convex from posterior suture to approximately beginning of siphonal canal, thence shallowly concave to anterior tip; growth lines and labral profile gently sigmoid, antecurrent at suture, concave aperturally below suture. Sculpture of evenly spaced, distinct, raised spiral straps separated by interspaces as wide as spirals, numbering 13 or 14 on last whorl, and about 10 low strong nearly straight, rounded axial ribs, well developed on posterior half of whorl, but obsolete on siphonal neck. Aperture elliptical; inner lip covered with a thin callus wash, unevenly excavated parietally, oblique and gently twisted to the left in its siphonal part, bearing one oblique, inconspicuous, laterally compressed fold at juncture of canal and aperture; outer lip incomplete in all specimens at hand, but apparently thin, transversely lirate internally at apertural margin but smooth farther within; columella rather short and twisted to the left distally; siphonal fasciole low, broad, rounded, smooth, enclosing minute umbilical chink.

Holotype: LACMIP cat. no. 11567.

Paratypes: LACMIP cat. nos. 11568–11569 from LACMIP loc. 10735 (= CIT loc. 1212).

Dimensions: See Table 10.

Type locality: LACMIP loc. 10735 (= CIT loc. 1212), Little Cow Creek, two miles (3.2 km) NE of Frazier Corners, Shasta Co., California.

Distribution: Known only from the type locality.

Geologic age: Turonian.

Remarks: *Skyles salsus* is described from three specimens. It resembles *Ornopsis glenni* Wade, 1926, the type species of *Ornopsis*, but differs in having the axial ribs persist to the posterior suture, lacking a concave subsutural band, having coarser, more widely spaced and fewer spiral ribs, and having a shorter siphonal canal.

Etymology: The species is named for its type locality on Salt Creek, Latin, *salsus*, meaning salted, salty, witty.

Subfamily FUSININAE Wrigley, 1927

Genus *Remera* Stephenson, 1941

Type species: *Remera microstriata* Stephenson, 1941, from the Maastrichtian of the Gulf Coast.

Diagnosis: Medium-sized fusiform shells with the spire more than half total shell height. Whorls flat sided, ornamented by strong collabral ribs and subdued overriding spiral ribbons. Aperture lenticular, angulated posteriorly; siphonal canal moderately long and straight; columella smooth (SOHL, 1964:226).

Discussion: *Remera* is represented by several species from the Gulf and Atlantic coastal plains *Exogyra ponderosa* and *Exogyra cancellata* zones. Specific differentiation within the genus is based, for the most part, on relatively minor differences in convexity of the whorl sides and sinuosity of the collabral ribs, and some species are based upon so little material that comparison is difficult. Some of these species may, with further study, prove to be synonyms (SOHL, 1964:226). *Remera* has not been reported hitherto from the Pacific Coast Cretaceous nor from beds as old as the Turonian.

ERICKSON (1974:207) suggests that *Remera* may be a synonym of *Exilia* Conrad, 1860, type species *Exilia pergracilis* Conrad, 1860, by monotypy, Paleocene, Gulf Coast. STEWART (1927) indicated that *Exilia* has a shallow posterior siphonal notch and placed *Exilia* in the Turridae, where most subsequent workers have left it. BENTSON (1940:202) was unable to find any indication of a posterior notch and placed it in the Fusininae, but *Exilia* continues to be classed as a brachytomine turrid (e.g., GIVENS, 1974:91). The growth line of *Remera* has a broad posterior sinus like that of other Fusininae. *Remera* has the spire equal to more than half the total shell height, whereas in *Exilia* the spire is relatively shorter, and the aperture is equal to or longer than the spire.

Remera vacca Saul & Popenoe, sp. nov.

(Figures 92–95)

Diagnosis: A small, short *Remera* with 15 collabral ribs.

Description: Shell small, slender, subfusiform, with rounded whorls and an acute spire; apical angle about 35°;

whorls about six (spire incomplete), gently and evenly convex, wider than high; suture linear and impressed; last whorl slightly less than one-half the height of the shell, evenly but broadly convex, rounding abapically into a straight and rather short anterior canal; growth lines forming a gentle parasigmoid curve, concave on posterior part of body whorl, convex toward aperture anteriorly, aligned nearly with the shell axis. Sculpture of about 15 low, sinuous, round-crested collabral ribs, and numerous, fine, irregularly spaced, incised spiral lines; collabral sculpture dying out at base of body whorl, but spiral lines persisting to anterior end of shell. Aperture elongate-fusiform, pointed posteriorly; inner lip smooth without visible columellar plications or callus, excavated at base of parietal wall; outer lip thin.

Holotype: LACMIP cat. no. 11570.

Type locality: LACMIP loc. 10764 (= CIT loc. 1446), south side Woodman Creek, Millville Quadrangle, Shasta Co., California.

Dimensions: See Table 11.

Distribution: Known only from the type locality approximately 152 m above the base of the Bellavista Sandstone Member of the Redding Formation.

Geologic age: Turonian.

Remarks: *Remera vacca* differs from all species previously assigned to this genus in being shorter. The spire does, however, make up more than half of the total shell height. This species is described from one well-preserved, nearly complete specimen, lacking only the apical and anterior sinus tips. If it is an adult, it is decidedly small for the genus.

Etymology: The species is named for its type locality in Little Cow Creek valley, Latin, *vacca*, meaning cow.

Superfamily VOLUTACEA Rafinesque, 1815

Family VOLUTIDAE Rafinesque, 1815

The Late Cretaceous seems to have been marked by an efflorescence of related large volutes in all parts of the world (DALL, 1907). In Dall's view, certain morphological types are repeated among the species making up the volute group in each fauna. The disparate morphologies of each local group are thus more closely related than they are to the forms they mimic of other areas. Dall, therefore, proposed taxa and generic groupings with strong geographic control, but others have chosen to group the species by morphological similarities. Although such incompatible methods have resulted in a classification of Cretaceous volutes that needs thorough revision, such is not attempted in this paper. Modern volutes have been reviewed by WEAVER & DU PONT (1970), who followed the classification of PILSBRY & OLSSON (1954), which divides the

Table 11
Measurements (mm) of *Remera vacca* sp. nov.

	H	D	Hp	Dp	Ha	A	La	Dp/ Hp
LACMIP								
11570	9.4*	4.0	1.9	2.8	4.9*	35°	4.2	1.5

* Specimen incomplete. Abbreviations decrypted in Introduction.

Volutidae into 12 subfamilies. PONDER & WARÉN (1988) combined some of the subfamilies of Pilsbry & Olsson, but added others and divided the Volutidae into 10 subfamilies. The least satisfactory of these is the Pholidotominae Cossmann, 1896, queried by Ponder & Warén, in which they questionably submerge Volutoderminae Pilsbry & Olsson, 1954. The four genera of Cossmann's Pholidotominae—*Pholidotoma* Cossmann, 1896, *Beisselia* Holzapfel, 1889, *Rostellites* Conrad, 1855, and *Gosavia* Stoliczka, 1866—have only the posterior growth-line sinus in common. *Pholidotoma* and *Beisselia* have a smooth columella and are probably not volutes. Cossmann's *Rostellites* includes *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877, and *Longiconcha* Stephenson, 1941, among others that PILSBRY & OLSSON (1954) place in Volutoderminae. PILSBRY & OLSSON (1954:29) suggest that *Gosavia* may be a turrid, but except for its growth line, its adult shell is similar to that of *Volutocristata* Gardner & Bowles, 1934, which Pilsbry & Olsson have included in Atheletinae Pilsbry & Olsson, 1954. *Volutocristata* has been shown to be a junior synonym of *Lyrischapa* Aldrich, 1911 (GIVENS, 1979), which is usually classed in the subfamily Fulgorarinae Pilsbry & Olsson, 1954.

Subfamily VOLUTODERMINAE Pilsbry & Olsson, 1954

The geologically oldest members of this subfamily have a marked posterior sinus to the growth line. The sinus is commonly on the shoulder in Cenomanian forms, but is generally broader, shallower, and closer to the suture in Maastrichtian forms. Sculpture may be strongly cancellate or *Ficus*-like, formed by the intersection of strong ribs and spirals.

Genus *Carota* Stephenson, 1952

Type species: By original designation, *Carota robusta* Stephenson, 1952, Cenomanian, from Woodbine Formation, Texas.

Diagnosis: Medium to large volutids with medium height spire; relatively large, strongly tilted protoconch; elongated, gracefully curved body whorl; coarsely noded shoulder angle; a deep notch at intersection of shoulder angle with outer lip; two or three coarse folds on columella; and a relatively fine pattern of spiral ornamentation.

Discussion: *Carota*, *Gosavia*, and *Rostellaca* Dall, 1907, have similar sculpture and growth line. *Gosavia* was assigned by STOLICZKA (1867) to the Conidae because of its shape and by COSSMANN (1896) and PILSBRY & OLSSON (1954) to the Turridae, presumably because of its growth line, but it has been accepted as a volute by many (e.g., DALL, 1907; WENZ, 1943). *Gosavia* has five to six columellar folds rather than the two or three of *Carota*. *Rostellaca* has three columellar folds, is shaped more like *Carota*, and has similar but rougher sculpture (DALL, 1907). *Rostellaca* differs mainly in having the posterior notch nearer the suture, a thicker, wider inner lip, and a strong twist to the end of the anterior siphon.

In *Carota*, STEPHENSON (1952) included, in addition to four species from the Woodbine Formation of Texas, *Volutoderma? venusta* Stephenson, 1936, from Banquereau Bank, off the east coast of Nova Scotia, and *Rostellites dalli* Stanton, 1893, from the "Pugnellus sandstone" of Turonian age, Huerfano Park, Colorado. The following two Pacific Slope species, *Scobinella dilleri* and *Cordiaera mitraeformis*, herein placed in *Carota*, have a posterior notch in the outer lip at the shoulder similar to that of *Carota*. This characteristic may prove to be an evolving trait. The relatively deep posterior notch distant from the suture is present in Cenomanian and Turonian volutes, a shallower notch closer to the posterior suture is common in later Cretaceous volutes, and most Cenozoic volutes have no more than a vestige of a notch against the suture.

The pattern of the columellar folds differs on the two Pacific Slope species: *Carota dilleri* (White, 1889) has three nearly equal, equally spaced folds as in the type species, *Carota robusta*; but in *C.? mitraeformis* (Gabb, 1869) the two posterior folds are closer together and the two anterior folds are stronger. Although fold number, placing, and strength vary among species assigned to *Carota* by STEPHENSON (1952), none has the same pattern as *C.? mitraeformis*.

Carota dilleri (White, 1889)

(Figures 96–101, 106, 107)

Scobinella dilleri WHITE, 1889:25, pl. 4, figs. 1–3; STANTON, 1895:19.

Volutoderma (Rostellinda) dilleri (White): DALL, 1907:10.

"*Scobinella dilleri*" White: STEWART, 1927:410.

Volutoderma dilleri (White): ANDERSON, 1958:175.

Rostellinda dilleri (White): JONES, SLITER & POPENOE, 1978: xxii.9, pl. 1, fig. 7.

Diagnosis: A slender, high-spired *Carota* with strongly shouldered, straight axial ribs, regular straplike spiral cords, and a relatively shallow growth-line notch at the shoulder.

Description: Shell of medium size, fusiform, with about seven volutions; whorls of the spire angulately convex; last whorl elongate, shouldered posteriorly, its greatest diameter near its shoulder, concave posterior to shoulder and broadly convex anterior to it, tapering anteriorly to a short siphonal canal; growth line opisthocline on ramp, strongly notched at shoulder, barely convex across flank. Spiral sculpture of coarse, raised, revolving lines or small ridges, about 17 or 18 on the last whorl, broader about middle of whorl, narrower anteriorly and on the siphonal neck, and obsolete on subsutural ramp; axial ribs present on all whorls, strongest at shoulder, usually nine on last whorl. Aperture narrow, nearly parallel-sided; anterior canal narrow, curved, flexed gently to the left; outer lip thin, with a broad sinus between suture and shoulder, broadly convex between shoulder and anterior siphon; columella with three strong folds of approximately equal size and spacing, strengthening interiorly; inner lip with pad of callus at posterior margin, adjacent to the anal gutter.

Syntypes: USNM cat. no. 20123 (3 specimens).

Hypotypes: LACMIP cat. nos. 10806 (= UCLA 59444, JONES *et al.*, 1978:fig. 7), 11571–11572, 11616; all from

Explanation of Figures 96 to 120

Unless otherwise indicated, figures are $\times 1$; specimens coated with ammonium chloride, except as noted.

Figures 96–101, 105–107. *Carota dilleri* (White, 1889). Figures 96–98, 107: LACMIP cat. no. 11571 from LACMIP loc. 10735, hypotype; Figure 96, aperture; Figure 97, back; Figure 98, right side; Figure 107, posterior growth line sinus at the shoulder, $\times 2$. Figure 99: LACMIP cat. no. 11616 from LACMIP loc. 10735, hypotype, aperture. Figures 100, 101: LACMIP cat. no. 10806 from LACMIP loc. 10735, hypotype; Figure 100, outer lip broken back, showing columellar folds; Figure 101, back. Figure 106: LACMIP cat. no. 11572 from LACMIP loc. 10735, hypotype, showing columellar folds, back view, uncoated.

Figures 102–105, 108–113: *Carota? mitraeformis* (Gabb, 1869). Figures 102–104, 113: LACMIP cat. no. 11573 from LACMIP loc. 10769, hypotype; Figure 102, aperture; Figure 103, back; Figure 104, right side; Figure 113, apical view. Figures 105,

108: LACMIP cat. no. 11618 from LACMIP loc. 10789, hypotype; Figure 105, left side; Figure 108, aperture. Figure 109: LACMIP cat. no. 11617 from LACMIP loc. 10789, hypotype, posterior growth line sinus at the shoulder, $\times 2$. Figure 110: LACMIP cat. no. 11574 from LACMIP loc. 10769, hypotype, section showing columellar folds, uncoated. Figures 111, 112: LACMIP cat. no. 10805 from LACMIP loc. 10789, hypotype; Figure 111, back; Figure 112, aperture.

Figures 114–120. *Konistra biconica* (Anderson, 1958). Figures 114–116, 120: CAS cat. no. 61935.01 from CAS loc. 61935, holotype; Figure 114, apical view; Figure 115, left side; Figure 116, right side; Figure 120, aperture. Figures 117–119: LACMIP cat. no. 11619 from LACMIP loc. 10789, hypotype; Figure 117, left side; Figure 118, aperture; Figure 119, posterior portion of growth line, $\times 2$. Photographs 96, 97, 100–103, 106, 110–112 by Susuki; 98, 99, 104, 105, 107–109, 113–120 by De Leon.

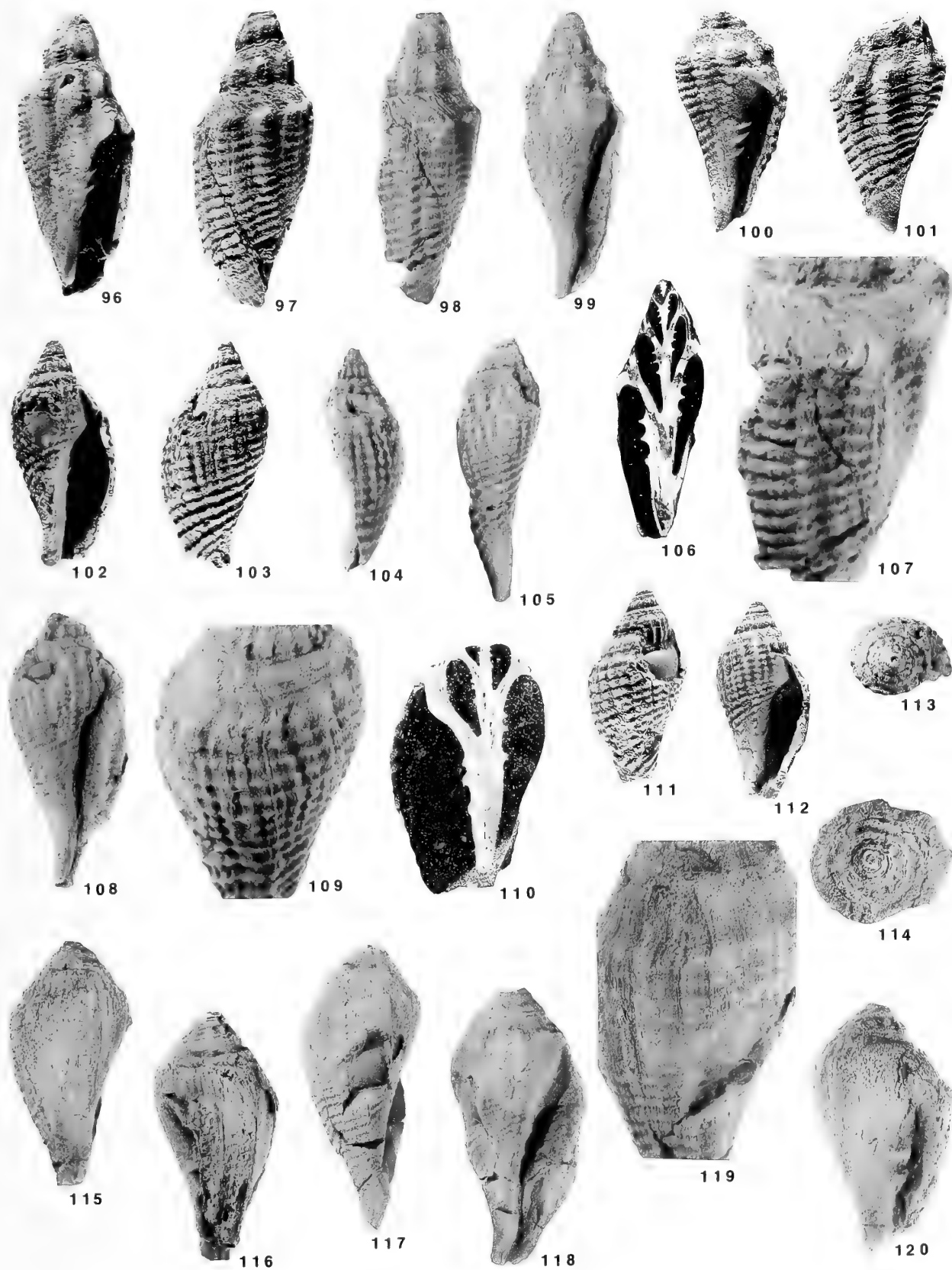


Table 12
Measurements (mm) of *Carota dilleri* (White, 1889) and *Carota? mitraeformis* (Gabb, 1869).

	H	D	Hp	Dp	Ha	Hs	A	R	Dp/Hp	Hp/Hs
<i>Carota dilleri</i>										
LACMIP 11571	49.0*	20.5	7.3	13.0	15.0*	3.0	49°	9	1.8	2.9
LACMIP 11572	45.0	—	6.7	—	—	3.3	41°	—	—	2.0
LACMIP 11616†	49.0*	18.8	7.2	12.6	13.5	3.4	53°	8	1.8	2.1
UCLA 59444	37.8*	20.4	—	—	—	—	—	8	—	—
<i>Carota? mitraeformis</i>										
MCZ 21856**	17.0*	9.5	—	—	—	—	—	—	—	—
LACMIP 11573	38.2	18.2	4.2	10.0	10.0	1.6	61°	23	2.4	2.6
LACMIP 11574	41.5*	27.0	—	—	—	—	—	—	—	—
LACMIP 11617	36.0*	18.0	4.7	10.0	7.0*	1.7	67°	19	1.9	2.8
LACMIP 11618	46.8*	20.4	4.5	12.0	8.0*	1.8	68°	16	2.7	2.5
UCLA 58445	34.0	16.4	4.9	9.4	10.0	2.8	59°	23	1.9	1.8

* Specimen incomplete; † specimen crushed; ** measurements *vide* STEWART, 1927. Abbreviations decrypted in Introduction.

LACMIP loc. 10735 (= CIT 1212), Little Cow Creek, 2 miles (3.2 km) NE of Frazier Corners, Shasta Co., California.

Dimensions: See Table 12.

Type locality: "Little Cow Creek valley, 18 miles (29 km) east of Redding, Shasta Co." (White, 1889).

Distribution: Nanaimo Group, unnamed formation of Sydney Island (Canada Geol. Surv. loc. 85511 and UW loc. 85900), British Columbia; Hornbrook Formation, Osburger Gulch Sandstone Member, Jackson Co., Oregon, and Siskiyou Co., California; Redding Formation, Frazier Siltstone Member above the horizon of *Romaniceras* (*Yubariceras*) *deverioide* (de Grossouvre, 1889), vicinity of Little Cow Creek, Shasta Co.; Gas Point Formation, Ono area, Shasta Co., California; Valle Formation, Upper Member, Cedros Island, Baja California, Mexico.

Geologic age: Early to late Turonian.

Remarks: DALL (1907) referred this species to *Rostellinda* Dall, 1907 (type species *Volutoderma* (*Rostellinda*) *stoliczkana* Dall, 1907, from the Trichinopoly Group of Southern India), a subgenus of *Volutoderma* Gabb, 1877. However, in characterizing *Rostellinda*, DALL (1907:6) says "the sinus near the suture," and neither he nor STOLICZKA (1867:87) mentions a notch at the shoulder that would produce a posterior emargination to the growth line similar to the posterior sinus of turrids. DALL (1907) based the type species of *Rostellinda*, *V. (R.) stoliczkana* Dall, 1907, upon figures of STOLICZKA (1867:pl. 7, figs. 6, 7 as *Fulgoraria elongata* d'Orbigny, 1843), and he assigned the nine specimens figured by STOLICZKA (1867:pl. 7) as *F. elongata* to five new species of *Rostellinda*. On none of these figures is a posterior growth-line emargination indicated at or near the shoulder. Stoliczka also figured and described *Gosavia indica* Stoliczka, 1867, a species which like the type species

of *Gosavia* Stoliczka, 1865, *Gosavia squamosa* (Zekeli, 1852), has a posterior notch at the shoulder and a resultant emargination of the growth line. WHITE (1889) had originally described *Carota dilleri* as a *Scobinella* Conrad, 1848, family Pleurotomidae, a placement doubtless suggested by the posterior growth line emargination. Dall either overlooked this characteristic of the growth line or did not consider it of systematic importance in reassigning *C. dilleri* to *Rostellinda*.

Figures of *Rostellaca zitteliana* (Holzapfel, 1888), type species of *Rostellaca* Dall, 1907, clearly show a posterior notch and emarginated growth line, but the notch and emargination are closer to the suture than in *C. dilleri*. DALL (1907) included four species from the Aachen chalk in *Rostellaca* which he characterized as having a "rougher sculpture, with nodulation of the intersections, the axial and spiral ridges more nearly equal in strength, the shell smaller, the shoulder less emphasized, and the posterior sinus less conspicuous."

Carota dilleri is similar to the type species *C. robusta* Stephenson, 1952, in overall shape and sculpture. *Carota dilleri* has a slightly higher spire, more regular spiral ribs, and a slightly shallower posterior siphonal notch than does *C. robusta*. *Carota dilleri* bears a greater resemblance to *C. robusta* than it does to *C. mitraeformis*. *Carota dilleri* differs from *C. dalli* STANTON, 1893 (p. 156, pl. 33, figs. 11-13), which is also of Turonian age, in having higher whorls and fewer axial ribs.

The growth line of *Volutoderma* (*Rostellinda*) sp. of YABE & NAGAO, 1928 (p. 95, pl. 17, fig. 16) Cenomanian or Turonian, from the Mikasa Formation, Horomui area of Hokkaido, is not illustrated. The specimen is incomplete, and may not be a volute. But the growth line on *Volutoderma* (*Rostellinda*) sp. of YABE & NAGAO, 1925 (p. 122, pl. 29, fig. 13, 13a, b) Late Cretaceous (*vide* HAYAMI & KASE, 1977:65, stage unknown), Cape Khoi beds in Alexandrovsk area of north Saghalin is described as being sinused on the shoulder, and the illustrated growth line

(pl. 29, fig. 13b) is similar to that of *C. dilleri* and *C. ? mitraeformis*. Unfortunately although suggestive of *Carota*, the specimen of YABE & NAGAO, 1925, is incomplete and the presence of columellar folds undetermined.

Both STANTON (1895) and STEWART (1927) considered *C. dilleri* to be similar to *Carota mitraeformis* (Gabb, 1869), and Stewart suggested that the latter species is the immature form of "*Scobinella*" *dilleri*. The two species are distinct, even in immature individuals, and apparently had different substrate preferences. At Redding, *C. dilleri* is common in the sandier facies of the Frazier Siltstone, but *C. mitraeformis* is found in the Bellavista Sandstone Member. *Carota dilleri* has fewer and stronger axial ribs, a higher and more strongly stepped spire, straighter inner lip, less strongly convex outer lip, stronger more equally developed and spaced columellar folds, a broader and more wrinkled whorl shoulder, and a callus pad on the posterior inner lip that is lacking in *C. mitraeformis*.

HAGGART (1991:A161) reports *Tragodesmoceras ashlandicum* Anderson, 1902, from Hamley Point, Sydney Island, British Columbia, and infers an early or mid-Turonian age for these deposits. *Carota dilleri* occurs above *Romaniceras* (*Yubariceras*) *deverioide* in the Redding area and thus probably ranges through most of the Turonian.

Carota ? mitraeformis (Gabb, 1869)

(Figures 102–105, 108–113)

Cordiera mitraeformis GABB, 1869:153, pl. 26, fig. 32.

Volutoderma mitraeformis (Gabb): STEWART, 1927:410, pl. 22, fig. 7; ANDERSON, 1958:174.

Volutomorpha mitraeformis (Gabb): JONES, SLITER & POPENOE, 1978:xxii.9, pl. 1, fig. 6 (*Volutoderma mitraeformis* on plate explanation).

Diagnosis: An almost pyriform *Carota* with about 15 axial ribs on the spire; axial ribs more numerous but reduced in strength to that of the spiral cords on body whorl.

Description: Shell medium sized, rather small for a volute; pleural angle about 65°; spire low, about ¼ the total length of the shell, with about four or five low angulately shouldered whorls; suture slightly impressed; ramp very steep, narrow, with concave band just posterior to shoulder; last whorl rounded, pyriform, with greatest diameter of whorl approximately one-third distance from suture to tip of anterior canal, and with narrow swollen subsutural band, narrow concave ramp, barely noticeable shoulder, and well-arched flank curving convexly to anterior tip of shell; last whorl of mature specimens encroaching posteriorly across preceding whorls giving a more obtuse apical angle to shell. Spiral and axial sculpture nearly equal on body whorl; spiral cords flat-topped, numbering 16 or 17 on body whorl, separated by interspaces approximately equal to cords in width; axial sculpture strongest on spire, about 16 ribs per whorl, variably developed, weaker on body whorl, strongest at shoulder; ribs about equal to cords posteriorly, diminishing anteriorly, and usually faint or absent on an-

terior half of whorl. Growth line with nearly straight trend perpendicular to suture but notched adjacent to suture and more deeply immediately posterior to shoulder at concave subsutural band, and having a slight retrocurrent deflection near columellar tip. Aperture elongate, ovoid with well-developed posterior groove at suture, terminating posteriorly in a narrow pointed siphonal canal; outer lip thin, smooth within, inner lip covered by a thin wash of enamel, shallowly excavated on parietal wall; columella gently flexed to the left at its tip, columellar folds three, posterior to middle of aperture, anterior and middle folds stronger and more distant, middle and posterior folds closer; no siphonal fasciole.

Holotype: MCZ cat. no. 21856.

Hypotypes: LACMIP cat. nos. 10805 (= UCLA 58445), 11617–11618 from LACMIP loc. 10789 (= CIT 1001), U.S. Highway 99, 4 miles (6.4 km) north of Redding, Shasta Co.; LACMIP cat. nos. 11573–11574 from LACMIP loc. 10769 (= CIT 1203), Dry Creek, Shasta Co., California.

Type locality: "Colusa Co., near the Hot Springs" (GABB, 1869).

Dimensions: See Table 12.

Distribution: Redding Formation, Bellavista Sandstone east of Redding, Shasta Co.; Great Valley Series near the Hot Springs, Colusa Co., California.

Geologic age: Early? Turonian, with *Tragodesmoceras*.

Remarks: Immature specimens of this species from the Redding area accord exactly with the figure and description of the holotype as given by STEWART (1927), and the Redding specimens are undoubtedly of the same species as the individual described by GABB (1869). Gabb reported this form from the "Shasta Group" (Early Cretaceous), but this age reference has been strongly questioned by STANTON (1895), STEWART (1927), and ANDERSON (1958), who considered the species to be of much younger age. Its occurrence in beds of Turonian age in the Redding area supports their opinion, and there is no evidence of its being collected from beds of Early Cretaceous age.

STANTON (1895) considered that *Carota ? mitraeformis* resembled *C. dilleri* (White) from the Late Cretaceous of Redding, and STEWART (1927) suggested that Gabb's species might be an immature individual of the latter. Both species occur abundantly at Redding, but *C. ? mitraeformis* is more common in the Bellavista Sandstone Member, and *C. dilleri* occurs in the Frazier Siltstone Member. *Carota ? mitraeformis* differs from *C. dilleri* in greater obliquity of columellar folds, which are unequally spaced and set deeper within the aperture, lower spire, weaker shoulder, and weaker axial ribs.

Among the forms from India illustrated by STOLICZKA (1867) as *Fulgoraria elongata* and named by DALL (1907), *Carota ? mitraeformis* most resembles *Rostellinda media* Dall,

1907 (STOLICZKA, 1867:pl. 7, figs. 4, 8, 9), but the illustrations of *R. media* do not indicate the presence of a posterior sinus at the shoulder, and its spiral sculpture is more widely spaced. As in the case of *C. dilleri*, the presence of the sinus in *C. ? mitraeformis* suggests that it should not be assigned to *Rostellina*. STEWART (1927) placed *C. ? mitraeformis* in *Volutoderma* Gabb, 1877, but that genus also lacks the posterior sinus at the shoulder and additionally has considerably more widely spaced spiral sculpture.

Carota ? mitraeformis is of smaller average size (although if complete, LACMIP cat. no. 11574 would probably be more than 50 mm high) and has a much less noticeable shoulder than species of *Carota* described by Stephenson from the Woodbine Formation of Texas. Although some adult specimens of *C. ? mitraeformis* approach *Conus* in shape, *C. ? mitraeformis* is more commonly shaped like a *Volutomorpha* Gabb, 1877, which lacks the posterior growth line sinus of *Carota*. The sculpture of *C. ? mitraeformis* resembles that of a *Volutomorpha* of SOHL's (1964) group B and has three oblique folds on the columella, the middle one of which is slightly the stronger. However, whereas *Volutomorpha* group B species have from one to three folds that are generally not all visible in the unbroken shell, the three well-developed folds of *C. ? mitraeformis* are visible, and the exterior of the shell shows no evidence of the total glaze coating that Sohl considers typical of *Volutomorpha*. All species assigned to *Volutomorpha* by Sohl are of geologically younger age than is *C. ? mitraeformis*; the placement of the columellar folds and the lack of glazing and posterior growth line sinus may be evolving features, and *C. ? mitraeformis* may be an early *Volutomorpha*. A more complete study of Cretaceous Volutidae is needed to clarify the generic placement of *C. ? mitraeformis*.

***Varens* Saul & Popenoe, gen. nov.**

Type species: *Varens formosus* Saul & Popenoe, sp. nov.

Diagnosis: Medium sized to moderately large volutes with moderately high spire; having shouldered whorls, a concave ramp, and a well-developed subsutural welt or collar, shoulder formed by posterior ends of axial ribs; last whorl broadly convex about periphery, gently concave anteriorly, tapering gracefully to a relatively long canal. Axial sculpture of ribs, pronounced and swollen at their posterior ends, diminishing anteriorly on last whorl, more strongly developed on earlier whorls, becoming shorter and knob-like on more mature whorls, diminished or obsolete on last whorl of large adults; spiral sculpture absent; exterior surface apparently coated with thin glaze. Growth lines gently retrocurrent at suture, forming a narrow posterior notch against previous whorl, nearly parallel to axis over mid whorl, gently antecurrent on siphonal neck. Aperture long and moderately narrow, outer lip thin; inner lip expanded parietally, nearly straight in columellar region; columella flexed to the left at anterior tip, bearing near

base of previous whorl, three oblique spiral folds; folds progressively stronger anteriorly.

Discussion: *Rostellites gracilis* STANTON (1893:157, pl. 34, figs. 1–3) from the "Pugnellus sandstone" of Huerfano Park and Poison Canyon, Colorado, may belong to this genus.

No previously described volute genus shares the characteristics of three folds, the anterior strong, posterior weak, lack of spiral sculpture, and exterior apparently coated by a glaze. *Volutomorpha* Gabb, 1877 (type species *Volutolithes conradi* Gabb, 1860, from Maastrichtian of New Jersey) is exteriorly glazed but has a low to moderate spire and is sculptured by spiral ribs. Like *Rostellana* Dall, 1907 (type species *Voluta bronni* Zekeli, 1852), *Varens* is relatively high spired, but *Rostellana* has the shoulder less well developed and lacks a glazed coating. *Carota* is of similar shape to *Varens* but has a growth line that is strongly sinused at the shoulder, lacks a glazed coating, and has spiral sculpture. *Fulgoraria* Schumacher, 1817 (type species *Voluta rupestris* Gmelin, 1791, Recent from Japan) is of similar shape to *Varens* but has four to eight folds on the columella, apparently a larger protoconch, and is spirally grooved.

Despite its scant spiral sculpture, *Varens* is placed in Volutoderminae because of its shape, number of columellar folds, and growth line. It resembles genera placed in Volutolithinae Pilsbry & Olsson, 1954, but has three columellar folds rather than the one fold of Volutolithinae. PONDER & WARÉN (1988) combined these two subfamilies as Volutoderminae.

Carota ? nodosa STEPHENSON, 1952 (p. 186, pl. 42, figs. 19–21) resembles *Varens* in shape, but it has spiral sculpture and a strong bend to the columella at the folds, and Stephenson mentions no external callus wash.

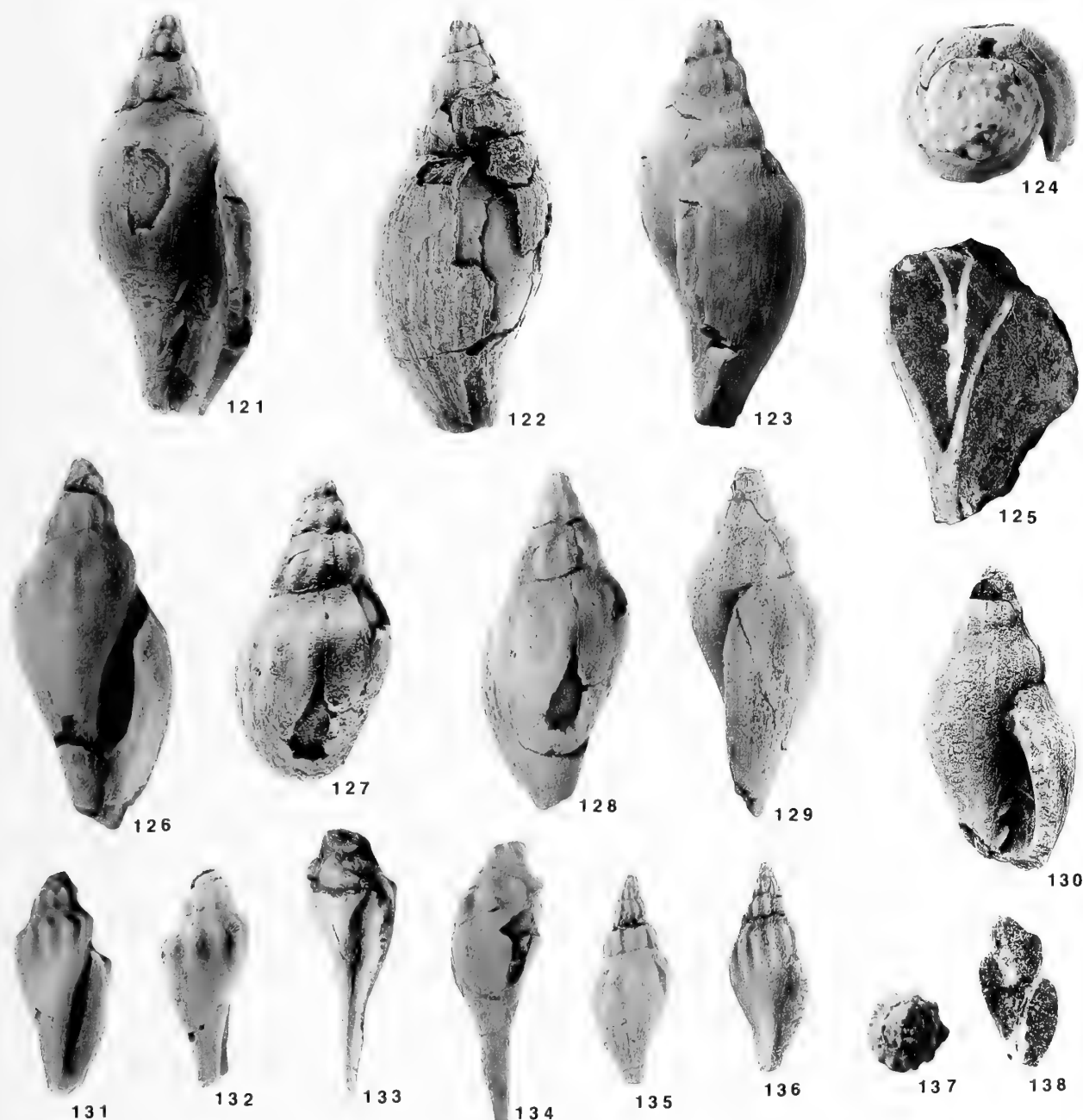
The generic name is derived from the name of a centurion in Caesar's army, Varenus, who was noted for a daring act of bravery. *Varens* is of masculine gender.

***Varens anae* Saul & Popenoe, sp. nov.**

(Figures 121–130)

Diagnosis: A large *Varens* having about ten axial ribs per whorl on spire, with rounded flank, and obsolete sculpture on mature whorls.

Description: Shell moderately large, broadly fusiform; apical angle about 49°; protoconch unknown; spire of five or six whorls, having a well-developed, narrow, subsutural collar, and concave ramp, expanding sharply to angulate shoulder; last whorl nearly smooth, broadly convex medially, gently concave anteriorly, tapering gracefully to nearly straight anterior siphonal canal. Growth lines gently retrocurrent at suture forming a narrow V-shaped posterior notch, nearly parallel to axis medially, gently antecurrent on siphonal neck. Sculpture of about ten axial ribs, pronounced and swollen on their posterior ends, di-



Explanation of Figures 121 to 138

Unless otherwise indicated, figures are $\times 1$; specimens coated with ammonium chloride except as noted.

Figures 121–130. *Varens anae* sp. nov. Figures 121–124: LACMIP cat. no. 11575 from LACMIP loc. 8195, holotype; Figure 121, aperture; Figure 122, back; Figure 123, right side; Figure 124, apical view. Figure 125: LACMIP cat. no. 11577 from LACMIP loc. 10886, paratype, section, showing columellar folds, uncoated. Figures 126–130: LACMIP cat. no. 11576 from LACMIP loc. 10886, paratype; Figure 126, aperture; Figure 127, back, anterior segment removed; Figure 128, back; Figure 129, right side; Figure 130, segment removed to show columellar folds.

Figures 131–138. *Varens formosus* sp. nov. Figures 131, 132: LACMIP cat. no. 11579 from LACMIP loc. 10891, holotype; Figure 131, aperture; Figure 132, left side. Figures 133, 134: LACMIP cat. no. 11580 from LACMIP loc. 10891, paratype; Figure 133, outer lip broken back, showing folds on columella and long anterior siphon; Figure 134, back. Figures 135–137: LACMIP cat. no. 11581 from LACMIP loc. 10891, paratype; Figure 135, back, $\times 2$; Figure 136, aperture, $\times 2$; Figure 137, apical view, $\times 2$. Figure 138: LACMIP cat. no. 11583 from LACMIP loc. 10891, paratype, section showing columellar folds, uncoated. Photographs 121, 122, 125, 127, 130 by Susuki; 123, 124, 126, 128, 129, 131–138 by De Leon.

Table 13
Measurements (mm) of *Varens anae* sp. nov. and *Varens formosus* sp. nov.

	H	D	Hp	Dp	Ha	Hs	A	R	Dp/Hp	Hp/Hs
<i>Varens anae</i>										
LACMIP 11575	62.0*	27.4	8.8	18.7	22.0*	4.4	49°	10	2.1	2.0
LACMIP 11576	56.4*	24.0	9.6	15.3	18.7*	5.5	47°	12	1.6	1.7
LACMIP 11577	42.0*	—	—	—	—	—	—	—	—	—
<i>Varens formosus</i>										
LACMIP 11579	36.0*	16.0	7.9	10.0	12.7*	5.0	46°	11	1.3	3.6
LACMIP 11578	26.2*	11.8	7.0	9.8	11.1*	4.5	43°	12	1.4	1.5
LACMIP 11580	43.0*	11.8	—	—	—	—	—	—	—	—
LACMIP 11581	16.6*	6.8	3.5	4.8	8.0*	2.3	40°	12	1.4	1.5
LACMIP 11582	16.5*	6.4	2.0	4.3	4.6*	1.4	42°	12	2.2	1.4
LACMIP 11583	23.8	—	—	—	—	—	—	—	—	—

*Specimen incomplete. Abbreviations decrypted in Introduction.

minishing anteriorly; ribs longer, narrower, and more strongly developed on earlier whorls, becoming progressively reduced, shorter and knoblike on later whorls and diminished on penultimate whorl and obsolete on last whorl. Aperture long, pinched posteriorly, expanded medially, contracted to the anterior siphon, outer lip thin, broadly and nearly evenly convex in outline; inner lip thin, parietal portion expanded, narrow on the columella; columella with three equally spaced, very oblique folds well within the aperture; anterior fold strongest.

Holotype: LACMIP cat. no. 11575.

Paratypes: LACMIP cat. no. 11558 from UCLA loc. 2325, Silverado Canyon; LACMIP cat. nos. 11576–11577 from LACMIP loc. 10886 (= CIT loc. 84), Santiago-Trabuco divide, Santa Ana Mts., Orange Co., California.

Type locality: LACMIP loc. 8195 (= CIT loc. 82), Silverado Canyon, Santa Ana Mts., Orange Co., California.

Dimensions: See Table 13.

Distribution: Ladd Formation, Baker Canyon Sandstone, Santa Ana Mountains, Orange Co., California.

Remarks: *Varens anae* differs from *Varens formosus* in having more rounded flanks especially in mature adults, which are considerably larger than any specimen of *V. formosus*. In specimens of *V. anae* and *V. formosus* that are of equivalent size, the shoulder of *V. anae* is less pronounced, the axial ribs are not as nodular at the shoulder, and the exterior seems less glazed, although this last may be a result of preservation. *Varens anae* differs from *Carota gracilis* (Stanton, 1893) of the *Pugnellus* sandstone, near Malachite and in Poison Canyon, Huerfano Park, Colorado, in being more slender.

Etymology: The specific name refers to the occurrence of this species in the Santa Ana Mountains.

Varens formosus Saul & Popenoe, sp. nov.

(Figures 131–138)

Diagnosis: A medium-sized, elongate, angulately shouldered *Varens* with about 11 axial ribs per whorl. Surface of shell apparently coated by glaze.

Description: Shell medium sized, elongately volutiform; apical angle about 46°; spire of about five whorls, having narrow subsutural welt, concave ramp, and angulate shoulder, and nearly straight flank constricted gently about base to form a broad siphonal neck. Growth line obscured by glaze, apparently nearly parallel to axis medially, slightly antecurrent on siphonal neck. Sculpture of about 11 axial ribs, strongest at shoulder, dying out anteriorly at about mid whorl; no spiral sculpture; shell surface apparently glazed. Aperture elongate; outer lip thin; inner lip thin, narrow, rounded posteriorly; columellar folds very oblique, anterior fold strongest, posterior very weak.

Holotype: LACMIP cat. no. 11579.

Paratypes: LACMIP cat. nos. 11578 from LACMIP loc. 10946, north side Silverado Canyon at the narrows; 11580–11583 from LACMIP loc. 10891 (= CIT loc. 1065), Ladd Canyon, just north of Silverado Canyon, Santa Ana Mts., Orange Co., California.

Type locality: LACMIP loc. 10891 (= CIT loc. 1065), Ladd Canyon, Santa Ana Mts., Orange Co., California.

Dimensions: See Table 13.

Distribution: Ladd Formation, Baker Canyon Sandstone, Santa Ana Mts., Orange Co., California.

Remarks: Specimens of *Varens formosus* are notable for their beautifully polished appearance. *Varens formosus* resembles *Carota dilleri* in shape but lacks spiral sculpture and the posterior sinus at the shoulder. *Varens formosus*

resembles young *V. anae* in which the bulbus adult whorls have not been formed. *Varens formosus* differs from *V. anae* in being smaller and more slender, in having a stronger shoulder, a less convex body whorl, and the posterior columellar plait barely present.

Carota? nodosa Stephenson, 1952, is similar in shape to *Varens formosus*, but *V. formosus* lacks spiral sculpture and has straighter axial ribs.

Etymology: The specific name is from Latin, *formosus*, meaning beautifully formed, comely, handsome.

Subfamily ATHLETINAE Pilsbry & Olsson, 1954

As adults, several Athletinae have a shell that becomes *Cassis*-like or strombiform. The body whorl may have a rounded or angled shoulder that may be unarmed or bear nodes or spines. The sculpture is more or less cancellate in the young, becoming partly or wholly smooth in adults.

Konistra Saul & Popenoe, gen. nov.

Type species: *Gosavia biconica* ANDERSON, 1958.

Diagnosis: A medium-sized, elongate pyriform volute with subsutural band, concave ramp, rounded shoulder, and rounded body whorl tapering to a broad anterior canal. Both axial and spiral sculpture present; axial sculpture strongest on early whorls, decreasing with maturity, and anteriorly over-ridden by spiral cords. Growth lines prominent, retrocurrent on subsutural band, scarcely flexed across flank. Aperture elliptical, outer lip thin; inner lip thin, expanded posteriorly; columella bearing about midway two well-developed, slightly oblique folds, flexed left and backward near its tip to form a well-developed anterior fasciole.

Discussion: Despite the number of middle Cretaceous volute genera already described, *Konistra* has a combination of features not found in any of them. In shape and sculpture *Konistra* resembles *Carota*, *Gosavia*, *Retipirula*, *Rostellaca*, *Rostellinda*, *Volutomorpha*, and *Volutoderma*. *Konistra* is most similar to *Gosavia* but has only two columellar folds, whereas *Gosavia* has five or six columellar folds and a deeply sinused growth line. *Konistra* tends to be shorter spired and more round shouldered than *Carota*, which has three columellar folds and a deeply sinused growth line. The sculpture of *Konistra* is not pustulose like that of *Retipirula*, which has two oblique folds and the trace of a third, and an anterior end to the siphon that is not strongly bent back and to the left. *Rostellaca* and *Rostellinda* are both higher spired than *Konistra* and have three folds on the columella. *Volutomorpha* has an overall surface glaze, a growth line that is strongly sinused adjacent to the suture, and one prominent fold on the columella rather than the two of *Konistra*. *Volutoderma* has three oblique columellar folds and a nearly straight tip to the anterior siphon.

The generic name is derived from Greek, *Konistra*, a

dusty rolling place. It refers to the presence of this genus at Sand Flat, Shasta Co., California, and is of feminine gender.

Konistra biconica (Anderson, 1958)

(Figures 114–120)

Gosavia biconica ANDERSON, 1958:175, pl. 75, figs. 3, 3a.

Description: Shell medium sized; pleural angle about 66°; spire low, about one-fifth the total length of the shell, with about five or six low angulately shouldered whorls; suture at or covering shoulder; ramp broad and shallowly sloping; last whorl pyriform, with greatest diameter of whorl just anterior to shoulder and approximately one-fourth the distance from suture to tip of anterior canal, with a relatively broad flat ramp, a subangulate shoulder, and well-arched flank curving convexly to constricted anterior siphonal neck; neck angled backward and to the left near its tip. Rough spiral and axial sculpture on body whorl; spiral cords unevenly spaced, numbering about 20 on body whorl, separated by interspaces of somewhat variable width but approximately equal to cord width; axial sculpture strongest on spire and at shoulder; ribs stronger than cords on fifth whorl, progressively weaker on subsequent whorls, about equal to cords posteriorly, diminishing anteriorly, usually faint or absent on anterior half of whorl, about 12 on fifth whorl, 10 on sixth, variably developed, weakest on body whorl. Growth lines prominent, with nearly straight trend perpendicular to suture but notched adjacent to suture and having a strong bend at anterior fasciole. Aperture elongate, ovoid with well-developed posterior groove at suture; outer lip thin, smooth within; inner lip expanded roundly onto body whorl, commonly encroaching above shoulder and exposed as a frill adjacent to suture; columella flexed backward and to the left near its tip; columellar folds two, just posterior to middle of aperture; siphonal fasciole moderately developed.

Holotype: CASG cat. no 61935.01.

Hypotype: LACMIP cat. no. 11619 from LACMIP loc. 10789 (= CIT 1001), sec. 7, T32N, R4W, Redding (1946) quadrangle, Shasta Co., California.

Type locality: CASG loc. 61935 [*ex* CASG 1294-A], "near the State highway, on Sand Flat," north of Redding, Shasta Co., California.

Dimensions: See Table 14.

Distribution: Known only from the vicinity of "Sand Flat." On 1913 U.S.G.S. Redding 30' Quadrangle, Sand Flat is between Buckeye and Salt creeks along U.S. highway 99, but is not designated on 1946 Redding 15' Quadrangle.

Geologic age: Turonian.

Remarks: In overall shape and sculpture *Konistra biconica*

Table 14
Measurements (mm) of *Konistra biconica* (Anderson, 1958).

	H	D	Hp	Dp	Ha	Hs	A	Dp/Hp	Hp/Hs
CAS 61935.01	43.7*	8.4	3.4	16.7	9.7	2.0	66°	4.9	1.7
LACMIP 11619	49.0*	21.4	5.2	5.0	6.9*	1.8	75°	0.97	2.9

* Specimen incomplete. Abbreviations decrypted in Introduction.

does resemble a *Gosavia*, but *K. biconica* has only two columellar folds rather than the five or six of *Gosavia* and lacks the growth line sinus present at the shoulder of *Gosavia squamosa* (Zekeli, 1852). *Konistra biconica* is superficially so similar to *Carota? mitraeformis* that the two are commonly mixed in collections, but *K. biconica* has one less fold on the columella, weaker sculpture, a nearly straight growth line, and a better developed anterior fasciole.

The specimen, CASG cat. no. 1552.03, referred to *Palaeatractus crassus* by ANDERSON (1958:42) has two columellar folds and resembles *Konistra biconica* except that the shoulder is well rounded and without angularity. Unfortunately the anterior end is broken and the shape of the anterior canal unknown. Specimen CASG cat. no. 1552.03 occurs with ammonites considered by MATSUMOTO (1960:80) to suggest late Campanian or early Maastrichtian age. The specimen is considerably larger than any other referred to *P. crassus*.

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LOCALITIES CITED

CIT and UCLA localities have been given LACMIP numbers. Most of the CIT localities of Turonian age in the Redding area were plotted on JONES *et al.* (1978:fig. 5). Most of the CIT localities of the northern Santa Ana Mountains were plotted on POPENOE (1942:fig. 2); these and UCLA localities were plotted on SAUL & BOTTJER (1982:maps 1–3). Many of the localities discussed in MATSUMOTO (1960) are also plotted therein.

Frazier Corners was almost a mile (1.6 km) northwest

of Bella Vista on the Redding (30') quadrangle, 1901 edition, reprinted 1913 and 1928, and also on the Shasta National Forest, California map of 1948. The Frazier Siltstone Member derives its name from Frazier Corners (HAGGART, 1986), and it serves as a reference point in several locality descriptions. However, on the Millville (15') quadrangle, 1953, and the Bella Vista (7.5') quadrangle, 1965, Bella Vista has been moved and replaces Frazier Corners.

- 82 CIT: = LACMIP 8195.
- 84 CIT: = LACMIP 10886.
- 92 CIT: = LACMIP 10100.
- 445 CASG: Fossils from Forty-nine mine, 2 miles (3.2 km) south of Phoenix, Jackson Co., Oregon. Hornbrook Formation. Late Turonian. (MATSUMOTO, 1960:77).
- 1001 CIT: = LACMIP 10789.
- 1032 CIT: = LACMIP 10726.
- 1042 CIT: = LACMIP 10876.
- 1065 CIT: = LACMIP 10891.
- 1164 CIT: = LACMIP 10079.
- 1195 CIT: (= UCLA 4416; LACMIP 10778) In bed of Stinking Creek, about midway between two north-south wire fences across creek, 2600'N, 1100'E of SE cor. sec. 6, T32N, R3W, Redding (1946) Quadrangle, Shasta Co., California. Coll.: Popenoe and Ahlroth, 21 June 1936. Redding Formation, Bellavista Sandstone Member. Early Turonian. (MATSUMOTO, 1960:104; POPENOE *et al.*, 1987:99).
- 1197 CIT: (= LACMIP 10776) Block of sandstone crowded with *Pugnellus manubriatus* picked up from stream bed of Stinking Creek, just downstream from first fence across creek upstream from the creek mouth, 4050'N, 44°W of SE cor. [2250'S, 2000'E of NW cor.] sec. 6, T32N, R3W, Redding (1946) Quadrangle, Shasta Co., California. Coll.: Popenoe & Ahlroth, 21 June 1936. Redding Formation, Bellavista Sandstone Member. Turonian. (JONES *et al.*, 1978:fig.5).
- 1203 CIT: (= LACMIP 10769) lens in sandstone cropping out in bed of Dry Creek, 700'S, 300'W of NE cor. sec. 6, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: Popenoe and Ahlroth, 23 June 1936. Redding Formation, near middle of Bellavista Sandstone Member. Turonian.
- 1207 CIT: = LACMIP 10810.
- 1209 CIT: = LACMIP 10771.
- 1212 CIT: (= LACMIP 10735) Little Cow Creek, Millville Quadrangle, Shasta Co., California.
- 1255 CIT: (= LACMIP 10744) French Creek north of Swede Basin.
- 1264 CIT: (= LACMIP 10759) Massive brown sandstone cropping out in bed of small gully tributary

- to Little Cow Creek, approx. 1805'S, 2250'E of NW cor. sec. 9, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 12 April 1937. Redding Formation, base of Melton Sandstone Member. Turonian. (MATSUMOTO, 1960:105).
- 1293D CASG: = CASG 61934.
- 1346 CIT: = LACMIP 10754.
- 1438 CIT: Highest sandstone bed under lava in gully on N side of Little Cow Creek, about ¼ mile (0.4 km) NE of Wilsey Ranch House, near NE cor. SW ¼ sec. 31, T33N, R2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 19 March 1940. Redding Formation, Bellavista Sandstone Member. Turonian.
- 1446 CIT: (= LACMIP 10764) Near top of N slope of hillside SE of Alturas-Redding Hwy, S side Woodman Creek, 2250'S, 500'W of NE cor. sec. 35, T33N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 23 March 1940. Redding Formation, Bellavista Sandstone Member. Turonian. (POPENOE *et al.*, 1987:99).
- 1552 CASG: South side of Antelope Valley, north end of Shale Hills, 500'W of center sec. 28, T26S, R18E, Kern Co., California. Coll.: G. D. Hanna and S. H. Shaw, April 1929. Panoche Formation. Late Campanian-early Maastrichtian. (MATSUMOTO, 1960:80).
- 1622 CIT: = LACMIP 10903.
- 2209 UCBMP: ?Sucia Island, San Juan Co., Washington. Cedar District Formation. Campanian.
- 2325 UCLA: Small gully entering Silverado Canyon from S, just W of the narrows, directly S of Holz Ranch house, about 1025'N, 150'E of SW cor. sec. 8, T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, 1946. Ladd Formation, top of Baker Canyon Sandstone. Turonian.
- 2360 CASG: "Devils Gate" on Berryessa Creek, 12,000 feet (3700 m) below top of Chico Group on Hamilton Ranch, near top of big conglomerate, Napa Co., California. Possibly Venado Formation. Turonian.
- 2757 USGS: Silverado Canyon, near mouth of Ladd Canyon, Santa Ana Mts., Orange Co., California. Coll.: S. Bowers, 23 April 1903. Ladd Formation, upper Baker Canyon Sandstone Member. Turonian.
- 2759 USGS: Near Silverado Canyon, in lower part of Ladd Canyon, Santa Ana Mts., Orange Co., California. Coll.: S. Bowers, 24 April 1903. Ladd Formation, upper Baker Canyon Sandstone Member. Turonian.
- 4214 UCLA: Soft thin-bedded sandstone exposed in channel of Little Cow Creek, SE cor. sec. 35, T33N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 2 September 1959. Redding Formation, Frazier Siltstone Member. Turonian.
- 4235 UCLA: Dip slope of Baker Canyon Sandstone on Black Star Quadrangle, cropping out about 0.3 mile (0.5 km) NW of old Holz Ranch house, 2600'N, 700'W of SE cor. sec. 7, T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Ladd Formation, Baker Canyon Sandstone Member. Late Turonian.
- 4252 UCLA: Banks of irrigation ditch at about 2450 foot (750 m) elev., W of and above SP RR tracks, W side of Bear Creek Valley, 2.8 mile (4.5 km) SE of Normal School Campus at Ashland, approx. 3100'N, 500'E of SW cor. sec. 24, T39S, R1E, Ashland Quadrangle, Jackson Co., Oregon. Coll.: W. P. Popenoe, 19 May 1944. Hornbrook Formation. Turonian.
- 5422 UCLA: Rancheria Gulch, about 1 mile (1.6 km) W of Henley, and approx. 400'N, 2000'W of SE cor. sec. 19, T47N, R6W, Yreka 30' Quadrangle (1939), Siskiyou Co., California. Coll.: W. P. Popenoe, summer 1951. Hornbrook Formation, Osburger Gulch Member. Turonian.
- 7199 UCLA: between Fremont Canyon and Oak Flat along a south fork of Fremont Canyon at about 1860 foot (570 m) elev., 350'N, 1050'E of SW cor. sec. 7, T4S, R7W, Black Star Canyon Quadrangle, northern Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe and J. E. Schoelhammer, 28 November 1952. Willams Formation, Pleasants Sandstone Member. Campanian.
- 7233 UCLA: Sulphur Creek, hard sandstone about 500 feet (150 m) upstream from abandoned cabin on east side of creek, NE ¼, SW ¼ (2500'N, 1750'E of SW cor.) sec. 23, T32N, R5W, Redding Quadrangle (1946), Shasta Co., California. Coll.: P. U. Rodda, summer 1956. Redding Formation, Bellavista Sandstone Member. Turonian.
- 7787 UCR: South side Silverado Canyon, elev. approx. 1340 feet (400 m), stream drainage directly below UCR loc. 7785, SW ¼, SW ¼ sec. 8, T5S, R7W, El Toro Quadrangle (1949), Santa Ana Mts., Orange Co., California. Coll.: Geol. 110 class, 8 November 1975. Ladd Formation, lower Holz Shale. Turonian.
- 7788 UCR: South side Silverado Canyon, elev. approx. 1370 feet (420 m), concretions in next stream drainage to south of UCR 7787 that leads to Silverado Creek, SW ¼, SW ¼ sec. 8, T5S, R7W, El Toro Quadrangle (1949), Santa Ana Mts., Orange Co., California. Coll.: Geol. 110 class, 8 November 1975. Ladd Formation, lower Holz Shale. Turonian.
- 8195 LACMIP: (= CIT 82) Limey sandstone bed near base of shale, S of roadcut at Holz Ranch

- (locality may become obscured by slides), Silverado Canyon [E edge SE $\frac{1}{4}$, SE $\frac{1}{4}$ sec. 7, T5S, R7W, El Toro Quadrangle], Santa Ana Mts., Orange Co., California. Coll.: B. N. Moore, 1927. Ladd Formation, Holz-Baker Canyon transition. Turonian.
- 10079 LACMIP: (= CIT 1164) S side Silverado Canyon near mouth of small N-flowing gully, and at top of lower fossiliferous sandstone series, about 400 feet (120 m) SE of Holz Ranch house in SE cor. sec. 7, T5S, R7W [1025'N, 150'E of SW cor. sec. 8], T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, 15 May 1935. Ladd Formation, Baker Canyon Sandstone Member. Turonian.
- 10100 LACMIP: (= CIT 92) Concretions in shale 100 feet (30 m) above stream and near fence on N side of Harding canyon, about $\frac{1}{4}$ mile (0.4 km) N of road fork in Santiago Canyon at Modjeska Canyon junction [near section line NW $\frac{1}{4}$, NW $\frac{1}{4}$ sec. 28, T5S, R7W, Santiago Peak Quadrangle] Santa Ana Mts., Orange Co., California. Coll.: B. N. Moore, 1928. Ladd Formation, basal Holz Shale Member. Turonian.
- 10726 LACMIP: (= CIT 1032) Shale outcrop on left bank of Dry Creek, E of road, 1.3 mile (2 km) N of Frazier's Corners, 1500'N of SE corner sec. 5, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 1933. Redding Formation, Frazier Silt. Turonian.
- 10735 LACMIP: (= CIT 1212) Little Cow Creek, approx. 2 mile (3.2 km) NE of Frazier's Corners, hard sandy concretions in shale, banks of gullies in pasture about 2500'N, 750'W of SE cor. sec. 4, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: Popenoe and Ahlroth, 7 July 1936. Redding Formation, Frazier Siltstone Member. Turonian. JONES *et al.* (1978:fig. 5).
- 10744 LACMIP: (= CIT 1255) W bank French Creek about $\frac{1}{2}$ mile (0.8 km) N of Swede Basin, 600'N, 600'E of SW cor. sec. 33, T33N, R2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 12 April 1937. Redding Formation, Bellavista Sandstone Member. Turonian.
- 10754 LACMIP: (= CIT 1346) Sandstone nodules in shale, left bank of Little Cow Creek, about 75 yards (70 m) NE (upstream) from intersection of creek bed with S line of sec. 9, and about $\frac{1}{4}$ mile (0.4 km) downstream from Walter Melton farmhouse, 10 mile (16 km) NE of Redding, 1500'N, 2200'E of SE cor. sec. 9, T32N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe and Jane Hoel, 8 July 1937. Redding Formation, Melton Sandstone Member. Turonian.
- 10771 LACMIP: (= CIT 1209) Oyster bed on left bank Salt Creek, about $\frac{1}{2}$ mile (0.8 km) N of gravel pits N of Alturas-Redding Hwy (U.S. 299), 1650'S, 1200'W of NE cor. sec. 34, T33N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: Popenoe and Ahlroth, 27 June 1936. Redding Formation, Bellavista Sandstone Member. Turonian.
- 10789 LACMIP: (= CIT 1001) West side of U.S. 99, 4.0 mile (6.4 km) by road N of Hwy 99 bridge just N of Redding over Sacramento River, sec. 7, T32N, R4W, Redding (1946) Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe and D. W. Scharf, 15 July 1931. Redding Formation, Bellavista Sandstone Member. Turonian.
- 10810 LACMIP: (= CIT 1207) Right side of Dry Creek, at Bellavista-Sherman Rd. crossing and 2.3 road miles (3.7 km) N of Redding-Alturas Hwy (U.S. 299) 2700'N, 50'W of SE cor. sec. 31, T33N, R3W, Millville Quadrangle, Shasta Co., California. Coll.: Popenoe and Ahlroth, 26 June 1936. Redding Formation, Bellavista Sandstone Member. Turonian.
- 10876 LACMIP: (= CIT 1042) Limey lenses in sandstone cropping out on N bank of Rancheria Gulch, about 1.5 mile (2.4 km) W of Henley, 210'S, 800'E of NW cor. sec. 30, T47N, R6W, Hornbrook Quadrangle, Siskiyou Co., California. Coll.: Popenoe and Findlay, 8 September 1933. Hornbrook Formation, Osburger Gulch Sandstone Member. Turonian.
- 10886 LACMIP: (= CIT 84) Sandstone above basal conglomerate. SW cor. of NE $\frac{1}{4}$ sec. 34, T5S, R7W, Santiago-Trabuco divide, Santa Ana Mts., Orange Co., California. Coll.: B. N. Moore, 1926. Ladd Formation, Baker Canyon Sandstone Member. Turonian.
- 10891 LACMIP: (= CIT 1065) Sandstone overlying basal Upper K conglomerate, from crest of scarp on W side of Ladd Canyon, about 0.6 mile (1 km) N of juncture of Ladd and Silverado canyons [1300'S, 300'E of NW cor. sec. 8, T5S, R7W, Black Star Canyon Quadrangle], Santa Ana Mts., Orange Co., California. Coll.: W. P. Popenoe, 3 March 1933. Ladd Formation, Baker Canyon Sandstone Member. Turonian.
- 10903 LACMIP (= CIT 1622): Soft gray sandstones cropping out along irrigation ditch 150–200 feet (46–61 m) above and to SW of Southern Pacific RR tracks about 4.0 mile (6.4 km) SE of U.S. Hwy 99 bridge over Ashland Creek, near midpoint of W boundary sec. 24, T39S, R1E, Ashland Quadrangle, Ashland, Jackson Co., Oregon. Coll.: W. P. Popenoe and W. A. Findley, 12 September 1933. Hornbrook Formation, Osburger Gulch Sandstone Member. Turonian.
- 15295 LACMIP: South side of Silverado Canyon near mouth of small N-flowing gully, about 400 feet

- (120 m) SE of Holz ranch house, 1025'N, 150'E of SW cor. sec. 8, T5S, R7W, El Toro Quadrangle, Santa Ana Mts., Orange Co., California. Coll.: Robert Drachuk, 1979. Ladd Formation, top of Baker Canyon Sandstone Member. Turonian.
- 61934 CASG: (= CASG 1293D) Near Frazier Corners, SW ¼ sec. 4, T32N R3W, Millville Quadrangle, Shasta Co., California. Coll.: C. M. Cross. Redding Formation, Frazier Siltstone Member. Turonian.
- 61935 CASG: (= CASG 1294-A): 4.6 miles (7.4 km) north of bridge at Redding, near the State highway, on "Sand Flat," Shasta Co., California. Coll.: F. M. Anderson. Redding Formation, Bellavista Sandstone Member. Turonian.
- 66549 CASG: Hagerdorn Ranch, 4 mile (6.4 km) NW of Montague, Siskiyou Co., California. Hornbrook Formation, probably Osburger Gulch Sandstone Member. Turonian.
- 85511 GSC: Hamley Point, Sydney Island, lat. 48°36'05"N, long. 123°16'05"W, British Columbia. Coll.: J. E. Muller, 21 August 1970. Nanaimo Group, near base. Turonian. (POPENOE *et al.*, 1987:100).

Atlanta californiensis, a New Species of Atlantid Heteropod (Mollusca: Gastropoda) from the California Current*

by

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Abstract. A new species of atlantid heteropod, *Atlanta californiensis*, from California Current waters off southern California is described on the basis of external and internal shell structure and eye, opercular, and radular morphologies. Although the external shell structure of *A. californiensis* is most similar to that of *A. gaudichaudi*, all other morphological features examined ally it most closely with *A. inflata*. The geographical distribution of *A. californiensis* is within the Transition Zone faunal province of the North Pacific Ocean. Other authors have rejected use of the radula as a taxonomic character in the Atlantidae. This is undoubtedly due to misinterpretation of differences within the radula that result from radular ontogenesis. When only the adult portion of the radula is used, interspecific differences are evident.

INTRODUCTION

In an extensive survey of the heteropod molluscan fauna of the California Current between about 24° and 44.5°N latitude, MCGOWAN (1967) reported five species of atlantids. In order of decreasing abundance, they included *Atlanta peroni* Lesueur, 1817, *A. lesueurii* Souleyet, 1852, *A. gaudichaudi* Souleyet, 1852, *A. inflata* Souleyet, 1852, *A. inclinata* Souleyet, 1852, and *A. turriculata* d'Orbigny, 1836. Specimens that could not be identified as one of the above species were referred to *Atlanta* sp. (J. McGowan, personal communication). Along with *A. peroni*, *Atlanta* sp. was the most abundant atlantid and ranged over nearly the entire CalCOFI station grid. The species of *Atlanta* described herein is the most abundant and often the only species of atlantid collected from the plankton off the coast of southern California (R. Seapy, unpublished data). Thus, it is

probable that a large portion of McGowan's *Atlanta* sp. is this previously undescribed species. Unfortunately, the specimens of atlantids from McGowan's study no longer exist (J. McGowan, personal communication).

Types and voucher specimens of *Atlanta californiensis* sp. nov. have been deposited in the Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH); California Academy of Sciences, San Francisco, California (CASIZ); National Museum of Natural History, Washington, D.C. (USNM); and Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF). Additional specimens are in the collections of A. L. Alldredge (ALA) and the authors (R. R. Seapy, RRS, and G. Richter, GR).

Atlanta californiensis Seapy & Richter, sp. nov.

(Figures 1–11)

Material examined: 134 juveniles, mature males and females, 0.7–2.5 mm diameter; CALIFORNIA, Santa Catalina

* Contribution 71, Ocean Studies Institute, California State University.

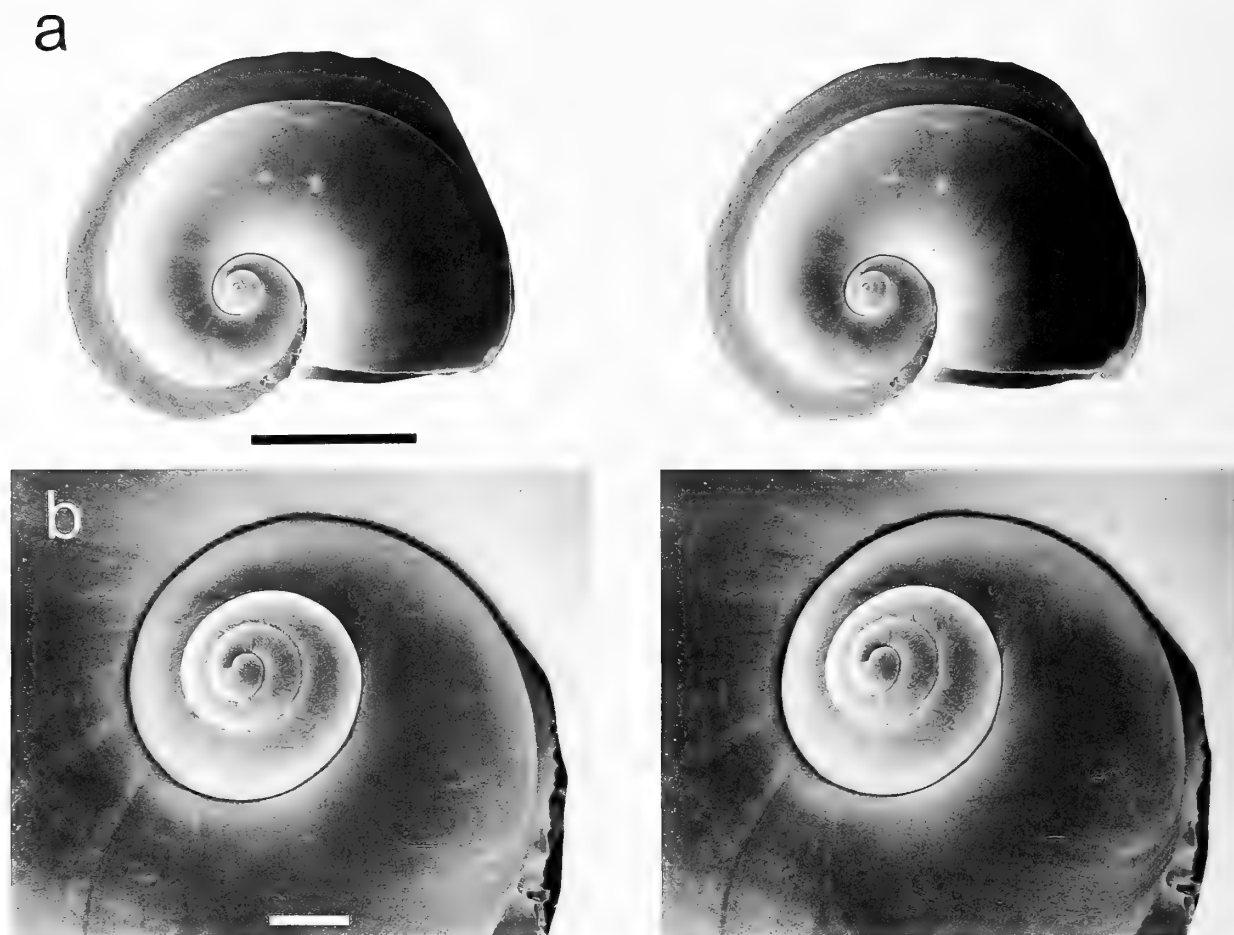


Figure 1

Atlanta californiensis sp. nov. Stereo-pair SEM photographs of holotype shell perpendicular to shell plane viewed from right side (2.48 mm, female; SBMNH 140126). Scale bars = a: 1.0 mm; b: 0.1 mm.

Basin, 33°03.4'N, 118°24.7'W, 0–150 m (oblique tow); coll. R. R. Seapy, California State University Ocean Studies Institute, R/V *Yellowfin*, 1-m plankton net (0.5-mm mesh), 29 August 1991, 1405–1435 hr; RRS (uncatalogued).

—766 juveniles, mature males and females, 0.6–2.7 mm diameter; CALIFORNIA, San Pedro Basin, 33°30.2'N, 118°25.5'W, 0–290 m (oblique tow); coll. R. R. Seapy, California State University Ocean Studies Institute, R/V *Yellowfin*, 3-m² plankton net (0.5-mm mesh), 13 August 1989, 1252–1400 hr; RRS (uncatalogued).

—126 juveniles, mature males and females, 0.6–3.2 mm diameter; CALIFORNIA, Santa Barbara Basin, 34°10'N, 119°45'W, 40 m (1800–1815 hr), 30 m (1830–1845 hr) and 15 m (2345–2400 hr); coll. A. L. Alldredge, University of California, Santa Barbara, R/V *Point Sur*, 70-cm BONGO nets (0.5-mm mesh), 4 October 1990; ALA (uncatalogued).

—8 mature males, 1.2–2.5 mm diameter; NORTH PACIFIC OCEAN, Subarctic Boundary, 43°15'N, 165°00'W, surface

neuston tow; coll. National Marine Fisheries Service personnel, R/V *Melville*, Station 108, Manta net (0.5-mm mesh), 22 October 1989, 1834–1849 hr; RRS (uncatalogued).

—2 juveniles and 2 mature females, 0.6–2.5 mm diameter; NORTH PACIFIC OCEAN, off British Columbia, 49°35'N, 127°44'W, 0–250 m (oblique tows); coll. Institute of Ocean Sciences, Ocean Ecology, Sidney, British Columbia personnel, Station SK-7, Cruise 9003, Series 28 (2.5-mm female) and Cruise 9006, Series 21 (remaining specimens), 70-cm BONGO nets, 16 October 1990; RRS (uncatalogued).

Diagnosis: A species of *Atlanta* Lesueur with a flattened, transparent calcareous shell and keel. Spire of shell low and globular; surface smooth, with 4¼ whorls; whorl width increases rapidly in fourth whorl. Suture separating spire whorls shallow. Umbilicus deep and wide. Last whorl encircled by keel that is high and truncate along its anterior margin.

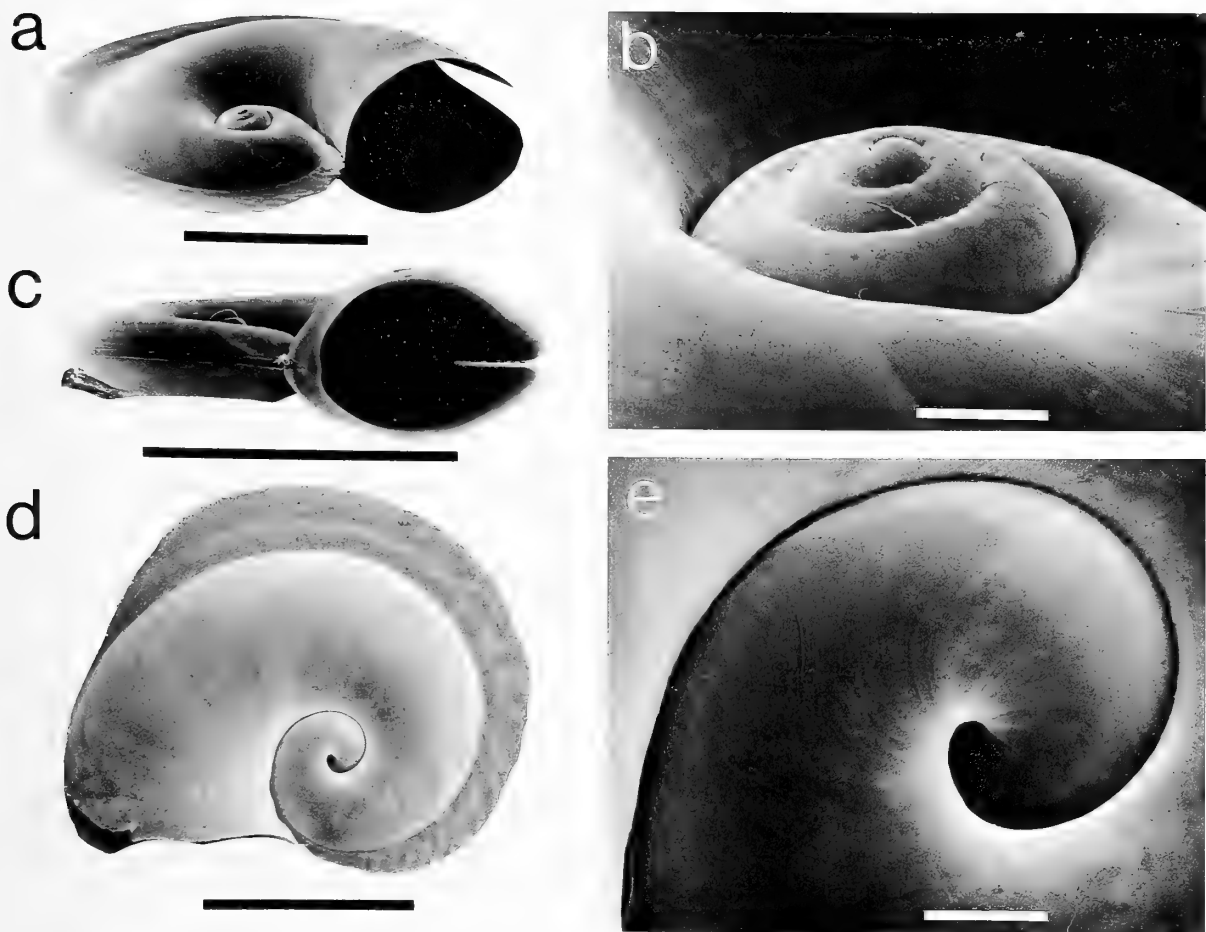


Figure 2

Atlanta californiensis sp. nov. a, b. Shell of holotype tilted at 50° angle. c. Apertural view of shell (1.6 mm male). d, e. Shell of paratype viewed from left side (2.1 mm male; SBMNH 140127). SEM photographs. Scale bars = a, c, d: 1.0 mm; b, e: 0.1 mm.

Description: *Shell* (Figures 1–3)—Shell moderately small; maximal diameter 3.5 mm, with $4\frac{2}{3}$ whorls. Keel penetrates between last and penultimate whorls in shells with diameter greater than about 2.0 mm (Figure 1). Keel base color orange-brown to red-brown. Spire low conical to globular in profile, lacking surface sculpture (Figure 2a–c). Spire coloration variable; either (a) clear to uniform light yellow, brown, or violet, or (b) light to dark mottled pattern of yellow-brown to brown. Spire suture coloration variable, ranging from clear to light violet to purple. Umbilicus wide, but narrows rapidly with penultimate whorls (Figure 2d, e). Inner walls of spire decalcified, whorls divided internally by thin, flexible chitinous membrane (Figure 3a). Larval metamorphosis occurs at shell diameter of 0.5–0.6 mm.

Operculum (Figure 4)—Operculum type “c” (after RICHTER, 1974); thin, transparent, oval in shape, with monogyre nucleus. Spiral portion of operculum lacks spines.

Eyes (Figure 5a)—Eyes type “a” (after RICHTER, 1974);

relatively small; clear, spherical lens; black pigmented base interrupted dorsally by triangular-shaped, unpigmented window. Distal portion of pigmented base lacking clear, transverse slit seen in type “b” eyes (Figure 5b).

Radula (Figures 6–8)—Radula large (relative to size of the animal), elongate and narrowly triangular; distinct sexual dimorphism. In males with shell diameter of 1.7–1.8 mm, length of radula about 700 μm , maximal width about 220 μm , with 75–80 rows of teeth and growth angle about 20–22°. In largest male examined (shell partially destroyed and shell diameter unknown), radula length almost 1000 μm , maximal width 260 μm , with 99 rows of teeth (Figure 6a). In male radula (Figure 7), central (rachidian) tooth with broad, low basal plate and relatively short single cusp that is always present. Lateral tooth with very broad, slightly curved basal plate, with one strong cusp at inner margin that points posteromedially. Squarish promontory of basal plate (characteristic of Atlantidae) forms a flattened hook at its posterior edge. Inner and

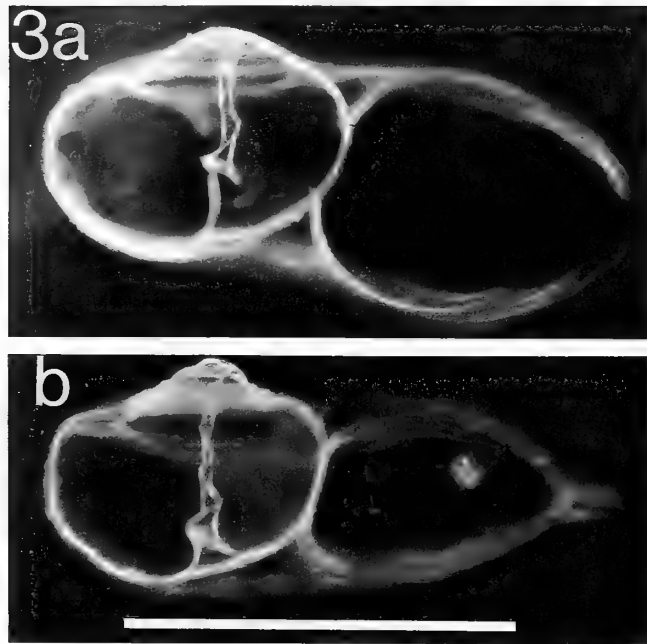


Figure 3. Shells of a, *Atlanta californiensis* sp. nov., and b, *A. inflata* (from tropical Atlantic). Immature specimens, frontal views. Transmitted light photographs. Scale bar = 0.5 mm.

outer marginal teeth approximately same length and somewhat shorter than corresponding lateral tooth. Marginal teeth long, slender, and gently curved toward tip, which is somewhat hooked.

In females with shell diameter of 1.7–1.8 mm, radula

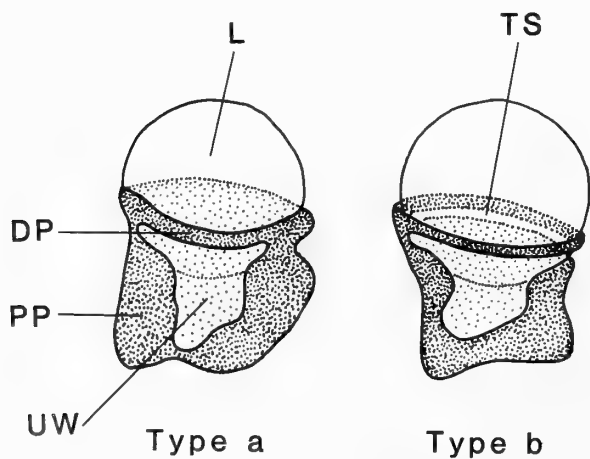


Figure 5

The two major eye types ("a" and "b") in atlantids (after SEAPY, 1990a:fig. 2 and RICHTER, 1974:fig. 3). Key: L, lens; DP, distal pigment; PP, proximal pigment; UW, unpigmented window; TS, transverse slit.



Figure 4. *Atlanta californiensis* sp. nov. "type c" operculum with monogyre nucleus (from 2.2 mm male). Transmitted light photograph. Scale bar = 0.5 mm.

700 μm in length (comparable with radulae from males of similar size), but maximal width (160–170 μm) about 55 μm less, growth angle (17–18°) about 4° less, and number of tooth rows (60–62) about 17 fewer. The major difference between radulae from mature males and females (Figure 8a, b) is width. Some differences in tooth morphology also exist; in females, basal plates of central and lateral teeth narrower, but distinctly higher, and marginal and lateral teeth shorter than in males.

Type material: **Holotype:** Shell of adult female, diameter 2.48 mm, mounted on SEM stub (Figures 1a, b, 2a, b), SBMNH 140126. **Paratypes:** Shell of adult male, diameter 1.60 mm, mounted on SEM stub (Figure 2d, e), SBMNH 140127. Preserved and dry specimens were deposited with the following museums: SBMNH 140128, 140129; CASIZ 088117, 088118; USNM 806324; and, SMF 309929, 309930.

Type locality: CALIFORNIA, Santa Catalina Basin, 33°03.4'N, 118°24.7'W, 0–150 m.

Etymology: The specific epithet is based on the geographical distribution of the species, which is largely restricted to the California Current (see distribution below).

Remarks: *Atlanta californiensis* appears to be most closely related to *A. inflata*, a very common circumtropical species. Like *A. inflata*, *A. californiensis* shows partial decalcification of the inner walls of the shell spire, type "a" eye

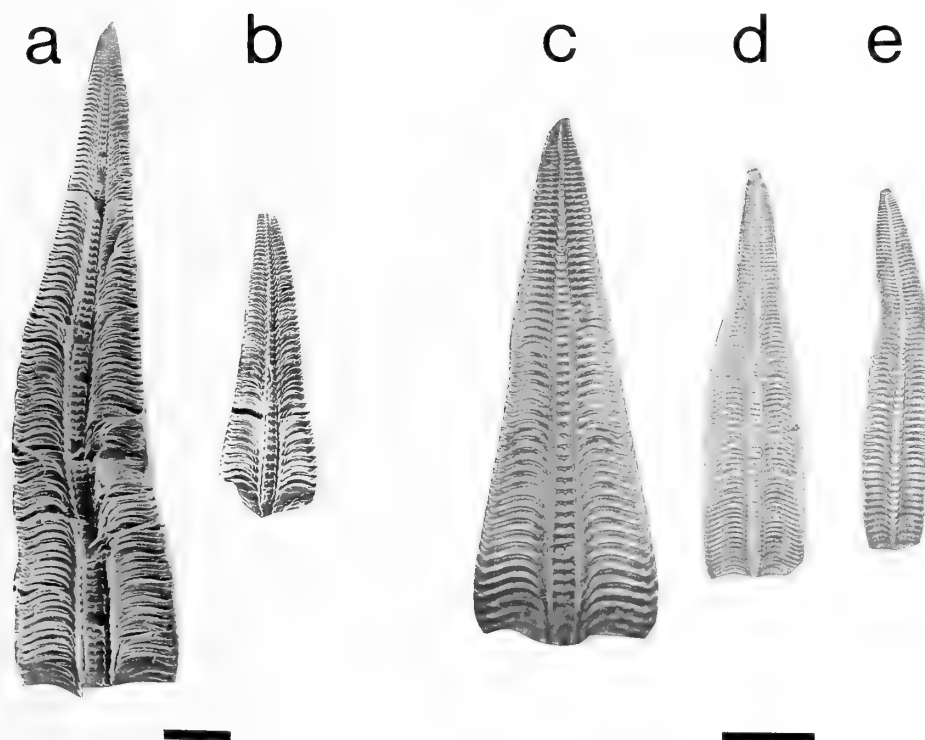


Figure 6

Complete radulae from *Atlanta californiensis* sp. nov. and *A. inflata* (from tropical Atlantic). SEM. a-c: *Atlanta californiensis*. a. Male with 99 tooth rows. b. Immature female with 56 tooth rows. c. Male with 68 tooth rows. d, e: *A. inflata*. d. Male with 98 tooth rows. e. Female with 80 tooth rows. a, b: SEM; c-e: transmitted light. Scale bars = a, b: 0.1 mm; c-e: 0.1 mm.

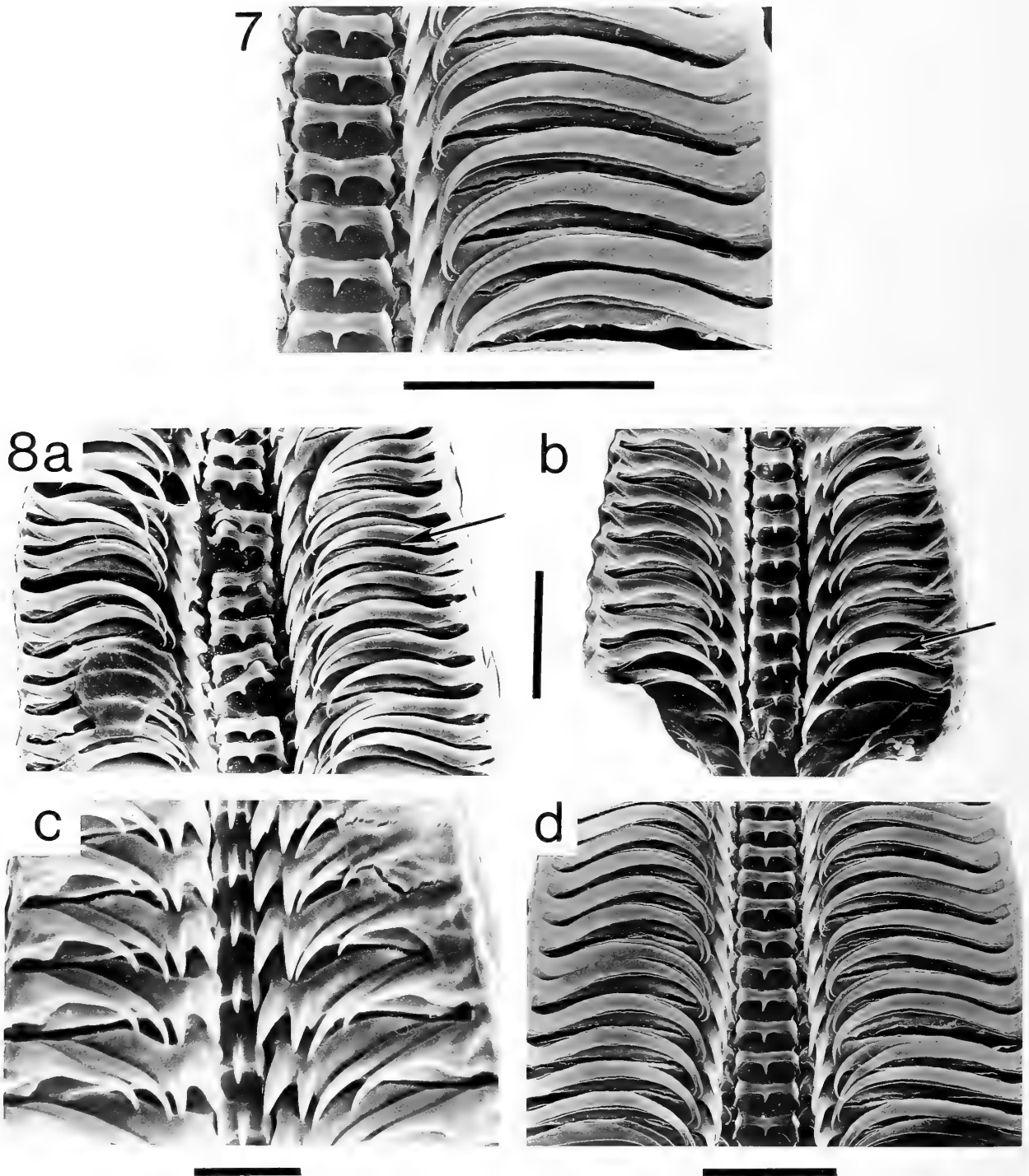
morphology, type "c" opercular morphology, sexual dimorphism of the radula, and similarities in the shape of the radular teeth and radular morphogenesis. The radulae of the two species differ, however, in that the radulae from both male and female *A. californiensis* (Figure 6a-c) are distinctly broader and consist of fewer tooth rows than the radulae of *A. inflata* (Figure 6d, e). The largest *A. californiensis* radula examined (Figure 6a) was from a large adult male and measured 1000 μm in length, with 99 rows of teeth. In contrast, the radula of the largest adult *A. inflata* examined by RICHTER (1987) was 590 μm in length, with 113 tooth rows. Although the radulae of both species are sexually dimorphic, the intersexual differences are greater in *A. californiensis*.

While the body and internal shell morphology of *Atlanta californiensis* are most similar to those of *A. inflata*, the external shell morphologies of the two species are quite different. The shell spire consists of about $3\frac{1}{4}$ whorls in *A. californiensis* and about $4\frac{1}{2}$ whorls in *A. inflata* (Figure 9a, b). The result of this difference is that the shell diameter of a specimen of *A. californiensis* at four whorls would be more than twice that of *A. inflata* at four whorls (Figure 10). The whorls of *A. californiensis* are more inflated and grow faster than those of *A. inflata*. These differences are

seen clearly by viewing the shells along the shell axis using transmitted light (Figure 3). The lack of sculpture on the spire whorls of *A. californiensis* contrasts with the raised spiral ridges on the spire of most *A. inflata* (Figure 10). This is a variable feature in *A. inflata*, however, since these ridges can be weakly expressed or even lacking (TESCH, 1909; RICHTER, 1987). Lastly, the umbilicus is wide in *A. californiensis* (Figure 2d, e) and narrow in *A. inflata* (RICHTER, 1987:figs. 9-12).

The external shell morphology of *Atlanta californiensis* is most similar to those of *A. gaudichaudi* and *A. peroni*. The three species have several features in common: (1) the shells have low spires that consist (Figure 9) of about $3\frac{1}{4}$ to $3\frac{1}{2}$ whorls, (2) the shell surfaces are smooth and lack surface sculpture, and (3) the sutures between the first and second whorls are shallow, while those between subsequent whorls are deeply incised (for *A. californiensis* see Figure 1b; for *A. peroni* see SEAPY, 1990a:fig. 4g, h; for *A. gaudichaudi* see NEWMAN, 1990:fig. 2b, c). Suture pigmentation in *A. californiensis* ranges from clear (similar to *A. peroni*) to light violet to purple (similar to *A. gaudichaudi*).

Distribution: Members of the family Atlantidae (Prosobranchia: Gastropoda) are predominantly tropical to sub-



Explanation of Figures 7 and 8

Figure 7. *Atlanta californiensis* sp. nov. Portion of radula from mature male, including (from left to right) central (rachidian), lateral, and marginal teeth. SEM. Scale bar = 50 μ m.

Figure 8. *Atlanta californiensis* sp. nov. a, b. Portions of radulae from mature male and female specimens, respectively. Arrows

indicate row 60 on each radula. c, d. Morphogenesis of male radula at cross-rows 10-14 and 69-80, respectively. Photographs from different radulae. SEM. Scale bars = a, b, d: 50 μ m; c: 10 μ m.

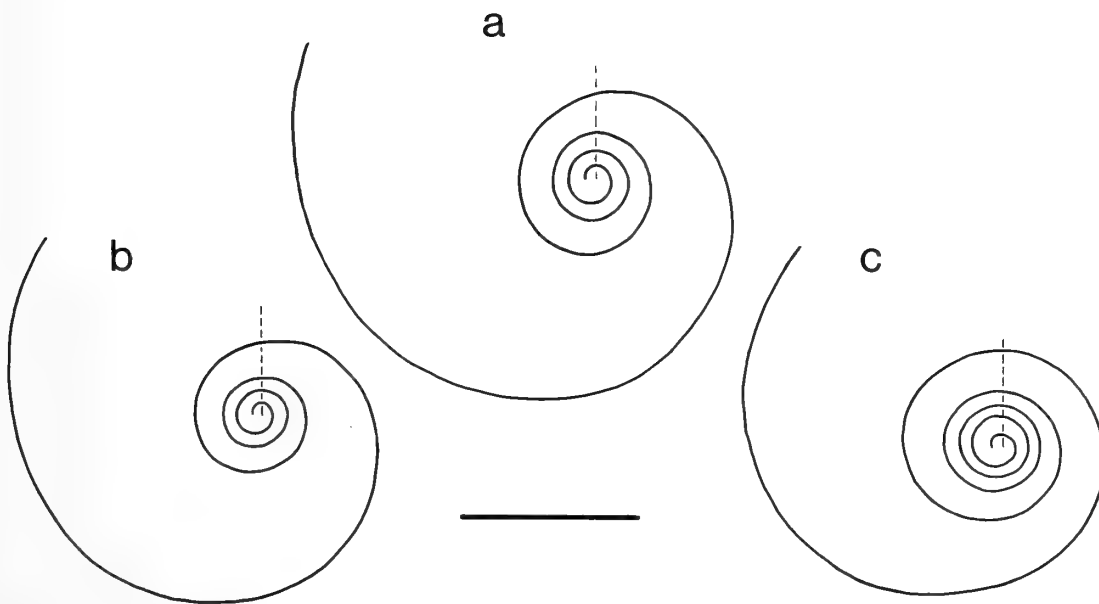


Figure 9

Sketches of shell spires from three species of *Atlanta* viewed from right side of shell. a. *A. californiensis* sp. nov. b. *A. inflata*. c. *A. gaudichaudi*. Sketches b and c after SEAPY (1990a:fig. 6). Scale bar = 0.5 mm.

tropical in distribution (THIRIOT-QUIÉVREUX, 1973). Most of the specimens of *Atlanta californiensis* collected to date, however, have come from temperate waters of the California Current off the coast of southern California. The California Current is a broad, sluggish and cold current that warms gradually as it flows southward off the Pacific coast of North America. Tropical to subtropical species of atlantids are encountered commonly only in the southern portion of the California Current, south of about 34°N (McGOWAN, 1967).

Biogeographically, the California Current comprises the southeastern portion of the Transition Zone faunal prov-

ince (Figure 11). This faunal province corresponds to the Transitional Domain of DODIMEAD *et al.* (1963), and extends southeastward in the California Current, northeastward in the Alaskan Current (to about 50°N) and westward across the North Pacific Ocean to Asia in a narrow (1–2° latitude) band located to the north of the Subarctic Boundary at about 40–41°N. The Transition Zone faunal province is bounded (Figure 11) by the Subarctic Pacific faunal province to the north, the Central North Pacific faunal province to the south, and the North American Continent to the east (FAGER & McGOWAN, 1963; McGOWAN, 1986).

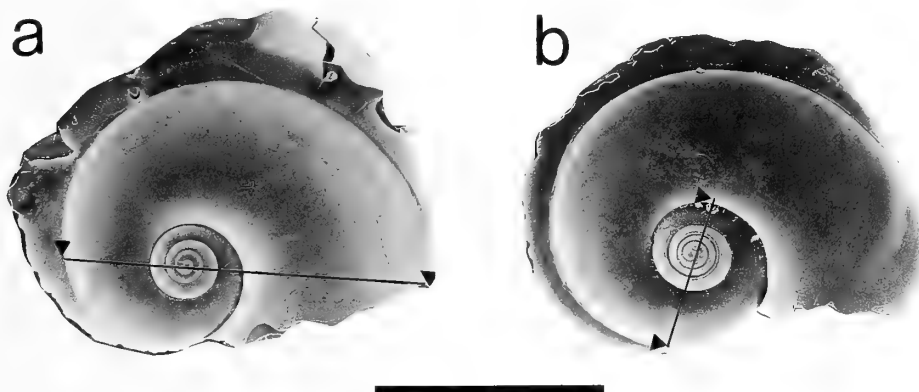


Figure 10

Shells of a, *Atlanta californiensis* sp. nov., and b, *A. inflata* (from tropical Atlantic). Lines between triangular marks indicate shell diameter at four whorls. SEM. Scale bar = 1.0 mm.

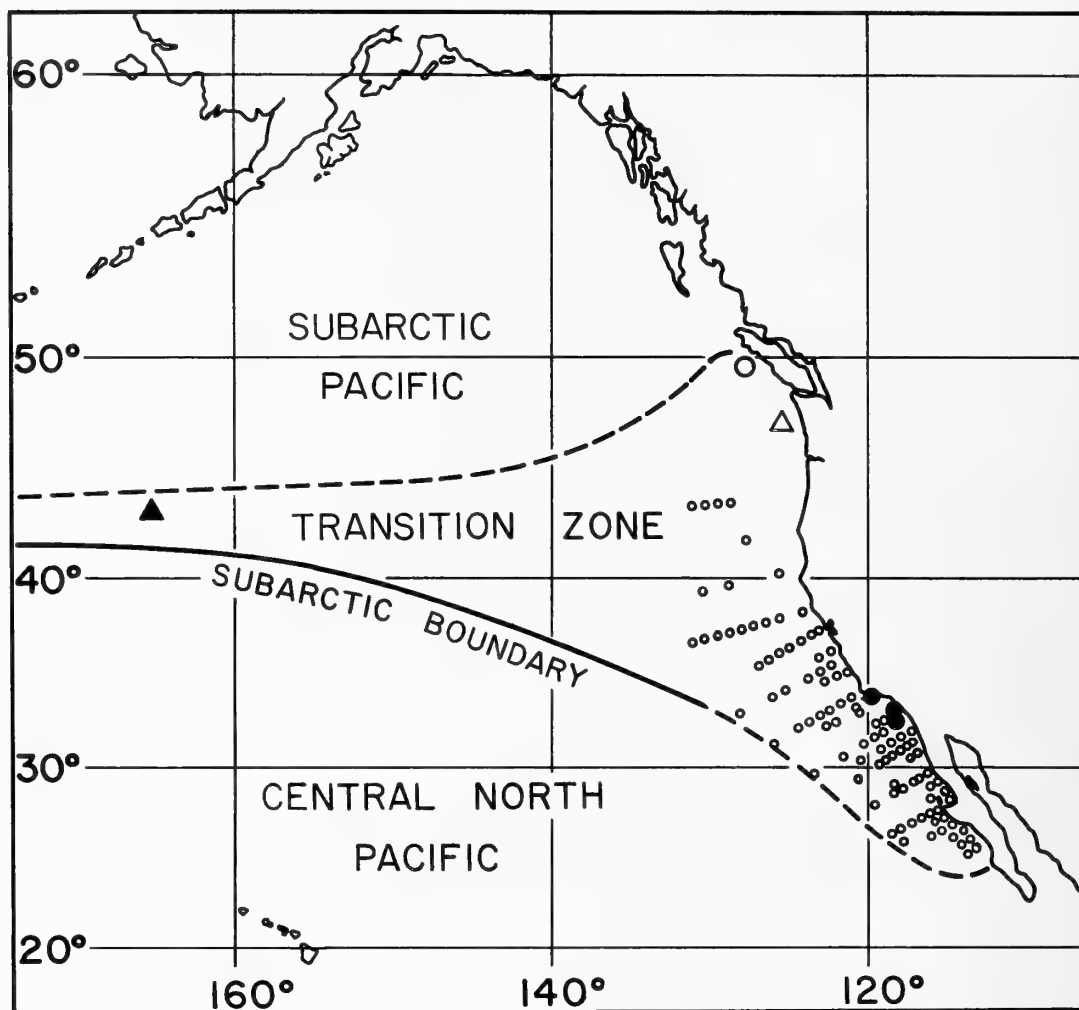


Figure 11

Biogeographical faunal provinces (Subarctic Pacific, Transition Zone and Central North Pacific) in the eastern North Pacific Ocean. Solid line denotes the Subarctic Boundary (after DODIMEAD *et al.*, 1963). Northern limits of Transition Zone indicated by dashed line (based on DODIMEAD *et al.* (1963:fig. 216). Southern limits of the Transition Zone defined by Subarctic Boundary and its southeasterly extension to Baja California (shown by dashed line; based on euphausiid distribution patterns in BRINTON, 1962). Collection records for *Atlanta californiensis* sp. nov.: large solid circles = southern California (San Pedro, Santa Catalina, and Santa Barbara basins); large open circle = oceanic waters off British Columbia; solid triangle = oceanic waters north of Subarctic Boundary. Open triangle = report of KOZLOFF (1987) for "*A. gaudichaudi*" from oceanic waters off Washington. Small open circles = records of MCGOWAN (1967) for *Atlanta* sp. from the California Current region off Pacific coast of North America.

Specimens of *Atlanta californiensis* have been identified by RRS from Transition Zone waters to the north of the Subarctic Boundary, oceanic waters off British Columbia, and three areas off southern California—San Pedro Basin, Santa Catalina Basin and Santa Barbara Basin (Figure 11). KOZLOFF (1987:208) reported that *A. gaudichaudi* "may be expected in oceanic plankton" off Washington. However, he qualified the identification by stating that it was "perhaps a form of *A. peroni*," although this remark could be based on a similar statement about *A. gaudichaudi* made by TESCH (1949:17). Because *A. gaudichaudi* was not recorded by MCGOWAN (1967) from California Current wa-

ters north of about 33°N and the shell of *A. californiensis* is most similar to this species (see above), we are reasonably certain that the species identified by KOZLOFF (1987) as *A. gaudichaudi* is actually *A. californiensis*.

The records of MCGOWAN (1967) for *Atlanta* sp. are included in Figure 11 because we consider that a large proportion of the specimens (certainly those collected north of about 34°N) that were relegated by McGowan to *Atlanta* sp. were *A. californiensis*. Our reasoning for this conclusion follows. Among the atlantids reported by MCGOWAN (1967) from the California Current, the only species that ranged to the north of 34°N were *Atlanta* sp. and *A. peroni*.

It is conceivable that McGowan misidentified *A. californiensis* as *A. peroni* under certain conditions (shells clear, spire and suture pigmentation absent), since the general shell morphologies of the two species are similar in that the spires consist of about $3\frac{1}{4}$ whorls and lack sculpture (discussed above). It is probable, however, that McGowan identified most *A. californiensis* as *Atlanta* sp., since most *A. californiensis* can be distinguished from *A. peroni* on the basis of spire coloration (normally clear, but occasionally light pink in *A. peroni* [SEAPY, 1990a]; yellow, brown, or violet, often with a mottled pattern in *A. californiensis*) and keel base coloration (clear, becoming golden-brown in *A. peroni* [SEAPY, 1990a]; orange-brown to red-brown in *A. californiensis*).

Based on the collection records in Figure 11, *Atlanta californiensis* is clearly a Transition Zone species. We are not aware of any records for *A. californiensis* from Subarctic Pacific or Central North Pacific waters. No collection records for any species of atlantids exist to our knowledge from Subarctic Pacific waters, and extensive collections of atlantids from Hawaiian waters (SEAPY, 1990a) have never recorded *A. californiensis*. A Transition Zone distribution has been characterized previously for only one other species of heteropod, *Carinaria japonica* (SEAPY, 1974).

The vertical distribution of *Atlanta californiensis* has not been resolved in detail. However, based on samples collected with opening-closing BONGO nets in San Pedro Basin (Seapy, unpublished data), the daytime vertical range appears to be largely limited to the epipelagic zone (surface to about 150 m off southern California). Opening-closing net samples have not been collected at night, and the question of whether or not nocturnal vertical migration takes place in this species remains to be determined. However, we suspect that upward nocturnal migration does occur since vertical migration was reported (SEAPY, 1990b) for other species of atlantids whose ranges also extended into the lower portion of the epipelagic zone off Hawaii.

An interesting aspect of the vertical distribution of *Atlanta californiensis* is that large numbers of individuals have been collected in surface samples taken with neuston nets on a number of occasions in San Pedro Basin (Seapy, unpublished data). The animals in these samples were exclusively males. Similar observations of high densities of male heteropods in the neuston were made by Richter (unpublished data) for three species—*Protatlanta souleyeti* (Smith, 1888), *A. oligogyra* Tesch, 1908, and *Firoloidea desmaresti* Lesueur, 1817—during Cruise 51 of the R/V *Meteor* in the central, tropical Atlantic Ocean during 1979. Heteropods are relatively uncommon in the neuston, but we have found that when they occur in high abundances most (if not all) of the individuals are mature males. These males do not appear to assemble in the uppermost water layer for feeding purposes, since their guts are usually empty (Richter, unpublished data). Perhaps this behavior is similar to that seen in mosquitoes, black flies, and other dipterans that exhibit aerial mating (reviewed by DOWNES, 1969). Males assemble in large swarms and individual females enter the swarm briefly to be captured by a male,

drop out of the swarm, and mate. This behavior functions to bring the sexes together from dispersed populations.

Discussion: *The radula as a taxonomic character*—The utility of the radula as a taxonomic character in the Atlantidae has been questioned and rejected by a number of workers (see below). We suggest that this rejection has resulted from a lack of understanding of radular ontogenesis. Since the teeth that are produced first are not cast off from the anterior end of the radula as they outwear their use, all growth stages of the radula are present in mature animals. As a consequence, the number of tooth rows increases continuously as the animal grows.

Because the shapes of the radular teeth change dramatically during ontogenesis, the radular characterizations given above apply exclusively to the mature portions of adult radulae. In most gastropods, morphogenesis of the radular teeth during ontogeny is restricted to the first few rows of teeth in the larval and post-larval animals (STERKI, 1893). In the Atlantidae, however, the transformation of tooth shapes continues for the greater part of radular growth (RICHTER, 1961, 1963).

The following characterization of morphogenetic changes in the radular teeth of *Atlanta californiensis* are applicable in principal to other atlantids. The teeth that are initially produced in the larva include a central rachidian tooth with a more-or-less square basal plate and a long, strong cusp. The corresponding lateral teeth are short and bi-, tri-, or even polycuspid. There is only one short marginal tooth on either side of the lateral teeth. In about rows 7 to 10 the second (outer) marginal teeth appear and the radula by now shows the regular taenioglossate tooth formula of $M_2M_1LRLM_1M_2$ (Figure 8c). At this stage of radular growth, there are no differences between males and females. The lateral teeth are strongly bicuspid and a rudimentary third cusp is present, but the third cusp disappears completely in the next few rows. The second (outer) cusp of the lateral teeth gradually decreases in size to an accessory denticle and then disappears altogether by about rows 50 to 60, generally later in females than in males. However, in males the teeth continue to change and attain their final shape after an additional 10 to 20 rows (Figure 8d).

From the above description of radular morphogenesis, it is clear that only the adult portion of the radula should be used as a taxonomic tool and that radular morphology is nearly useless when applied to juvenile specimens. Earlier workers presumably did not appreciate the complexities of radular morphogenesis, which would explain why a number of them (e.g., BUCHMANN, 1924; TESCH, 1949; VAN DER SPOEL, 1976) concluded that the radula is of no taxonomic importance in the Atlantidae.

ACKNOWLEDGMENTS

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The Gastropod *Terebra santana* Loel & Corey, 1932, from the Lower Miocene Vaqueros Formation, Southern California, Belongs in the Cerithiid Genus *Clavocerithium* s.s.

by

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Abstract. Re-examination of the primary type material and numerous other specimens of the gastropod *Terebra santana* Loel & Corey, 1932, which is locally very abundant in the lower Miocene Vaqueros Formation of California, reveals that the species is a cerithiid belonging to the genus *Clavocerithium sensu stricto*. This is the first report of *Clavocerithium* s.s. in the New World and its first record in rocks younger than Eocene. *Clavocerithium* (*Clavocerithium*) *santanum* is reported for the first time from the Vaqueros Formation in the upper Sespe Creek area, Ventura County, southern California.

INTRODUCTION

LOEL & COREY (1932), in their monographic study of the lower Miocene Vaqueros Formation in California, named and briefly described the gastropod *Terebra* (Subgenus = ?) *santana* LOEL & COREY (1932:236–237, pl. 47, figs. 8a, 8b, 9, 10, 11). They reported that this Vaqueros Formation species is very abundant wherever present. SCHOELLHAMER *et al.* (1981), BLUNDELL (1983) and DANIEL (1989) also reported very abundant specimens of this gastropod from various outcrops in the southern California area. These reports of such great abundance of a *Terebra* suggested that it had been misidentified as to genus, because modern *Terebra* is a predatory gastropod and makes up a small part of the populations of modern molluscan communities; one would expect it to be similarly uncommon in the fossil record. John G. Vedder and Wendell P. Woodring in SCHOELLHAMER *et al.* (1981) put the genus name in quotation marks when referring to “*Terebra*” *santana* because they had reservations about using this genus name.

The purpose of this report is to show that Loel & Corey’s *Terebra santana* is a cerithiid and not a terebrid. Examination of the holotype and three paratypes of *T. santana*, as well as numerous other specimens from southern California, revealed that this species belongs to the cerithiid genus *Clavocerithium* Cossmann, 1920.

The locally great abundance of Loel & Corey’s species fits in well with what is known about cerithiids. Modern species are very abundant in places like tidal flats. For example, I have observed scattered, densely packed patches of *Certhium stercusmuscarum* Valenciennes, 1832, on the tidal sandflat at San Felipe, Baja California, Mexico. BRUSCA (1980) and SCHMIDT (1987) reported that this species is extremely common on tidal flats in the northern Gulf of California, and specimens aggregate in gigantic clumps wherever a semihard sandy substrate is available. The specimens of *Clavocerithium* (*C.*) *santanum* (Loel & Corey) in the Vaqueros Formation are always in the near-shore-marine lower part of the formation, where there is gradation with the coastal-plain deposits of the underlying Sespe Formation. The specimens of *C. (C.) santanum* in the lower Vaqueros Formation are probably associated with tidal flats and nearshore storm-related lag deposits that developed in this zone of gradational nonmarine and marine environments. One of the paratypes of this species was reported by LOEL & COREY (1932:79) as possibly coming from an estuarine deposit.

Abbreviations used for catalog and/or localities are: CSUN, California State University, Northridge; LAC-MIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, UCMP, University of California Museum of Paleontology (Berkeley). Localities cited in this report are described under “Localities Cited.”

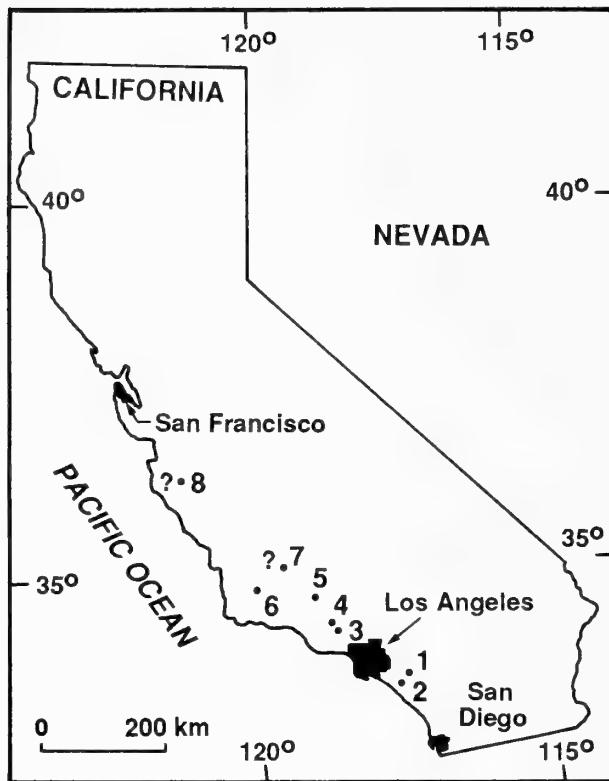


Figure 1

Geographic distribution of *Clavocerithium (C.) santanum* (Loel & Corey, 1932). Localities are numbered from south to north. (1) Santa Ana Mountains, Orange County; (2) San Joaquin Hills, Orange County; (3) Big Mountain, north side of Simi Valley, Ventura County; (4) Oak Ridge area, Ventura County; (5) Upper Sespe Creek, Ventura County; (6) Near Buellton, Santa Barbara County; (7) Eagle Rest Peak area, Kern County; (8) Junipero Serra Peak region, Monterey County. Question mark ("??") denotes tentative identification by LOEL & COREY (1932). The upper Sespe Creek area (No. 5) is a new report for this species.

COMMENTS ON GEOGRAPHIC DISTRIBUTION

LOEL & COREY (1932) reported that this species, *Clavocerithium (C.) santanum*, ranged from Orange County to Santa Barbara County, southern California. They also reported that the species may be present in central California, as far north as Monterey County (Figure 1). The type locality (locality UCMP 6128) is in Arroyo Trabuco in the southern part of Plano Trabuco, southern Santa Ana Mountains, Orange County. The exact location of this UCMP 6128 is not known, but I visited the general area and found specimens of *C. (C.) santanum* in greenish-gray to reddish-gray exposures of very fine-grained sandstone that apparently are in the zone of intergradation between the lower part of the Vaqueros Formation and the upper part of the Sespe Formation.

Other workers (SCHOELLHAMER *et al.*, 1981; DANIEL,



Figure 2

A hand specimen (hypotype LACMIP 12102) showing the dense packing of *Clavocerithium (C.) santanum* (Loel & Corey, 1932) at locality CSUN 1185, Hicks Canyon, northern Santa Ana Mountains, Orange County, southern California. Magnification is $\times 1.1$.

1989) have confirmed the presence of *Clavocerithium (C.) santanum* in the Santa Ana Mountains. DANIEL (1989) found several beds in Hicks Canyon in the Santa Ana Mountains, where specimens constitute as much as 50% of the rock. I visited this area and also found scattered, densely packed concentrations at locality CSUN 1185 (Figure 2).

BLUNDELL (1983) reported this species from several localities in the Big Mountain area, north side of Simi Valley, southern California. His specimens are stored in the CSUN collection. Only at locality CSUN 555 are the specimens sufficiently well preserved to be identified as *Clavocerithium (C.) santanum*. All of the specimens that Blundell collected from other localities in the area are poorly preserved and could only be identified as certhiaceans. LOEL & COREY (1932) did not report their species from the Big Mountain area.

REID (1978) and SQUIRES & FRITSCH (1978) reported abundant specimens of the potamidid gastropod *Potamides sespeensis* Loel & Corey, 1932, from numerous CSUN localities in the Vaqueros Formation, upper Sespe Creek area, Ventura County, southern California, but upon re-examination the specimens from CSUN 428 proved to be *Clavocerithium (C.) santanum*. This is the first documented report of this species from this area. At most of the other localities, specimens are poorly preserved and could only be identified as certhiacean. *Potamides sespeensis*, with its distinctive noded ornamentation and spiral ribbing, was collected from localities CSUN 159 and 401. BADGER (1957) tentatively reported this species from the Sespe Creek area. His collections are now stored at LACMIP; the specimens are poorly preserved but appear to be *C. (C.) santanum*.

SYSTEMATIC PALEONTOLOGY

Family CERITHIIDAE Fleming, 1822

Subfamily CERITHIINAE Fleming, 1822

Genus *Clavocerithium* s.s. Cossmann, 1920

Type species: By original designation *Cerithium lacazei* "Vasseur" Cossmann, 1897, 1898, upper? Eocene of the Lower Loire River area, Brittany, northwestern France. See HOUBRICK (1978) for a discussion of the authorship of this species.

Clavocerithium (Clavocerithium) santanum
(Loel & Corey, 1932)

(Figures 3–12)

Terebra (Subgenus = ?) *santana* LOEL & COREY, 1932:236–237, pl. 47, figs. 8a, 8b, 9, 10, 11).

Terebra santana Loel & Corey, 1932: KEEN & BENTSON, 1944:200.

Supplementary description: Shell small in size (up to 26.5 mm height), elongate, high-spired, approximately 11 whorls, solid. Suture distinct, slightly channeled. Protoconch low, conical? shape. Upper spire whorls straight sided to slightly convex for the first 3 to 15 mm in height (usually just the first 6 mm), grading into tabulate whorls, lower spire whorls and body whorl prominently tabulate, rarely convex; each whorl taller than the previous whorl. Upper and middle spire whorls with 4 to 5 moderately heavy, equidistant spiral ribs (rarely preserved), anterior-most spiral rib situated in sutural area. Penultimate and body whorls smooth. Aperture oblique, small, approximately $\frac{1}{6}$ to $\frac{1}{4}$ of shell length. Columella concave with central oblique plait that coincides in position with columellar side of anterior canal; thin to moderately thick columellar callus detached along outer side. Outer lip sinuous, and growth lines on body whorl sinuous. Anterior canal short but distinct, slightly reflexed backward.

Type material and type locality: Holotype, UCMP 31608 and paratypes, UCMP 31609 and 31610, all three from locality UCMP 6128, Trabuco Canyon, Santa Ana Mountains, Orange County, southern California; paratype, UCMP 31611, locality UCMP A-253, Wiley Canyon, Oak Ridge area, Ventura County, southern California.

Geologic range: Early Miocene.

Distribution: Vaqueros Formation, southern California, and tentatively central California: Santa Ana Mountains, Orange County (LOEL & COREY, 1932; SCHOELLHAMER *et al.*, 1981; DANIEL, 1989); San Joaquin Hills, Orange County (LOEL & COREY, 1932); Wiley Canyon in Oak Ridge area and near mouth of Grimes Canyon, eastern Ventura County (LOEL & COREY, 1932); Big Mountain, northern Simi Hills (BLUNDELL, 1983); upper Sespe Creek, Ventura County (herein); western Santa Ynez Mountains, Santa Barbara County (LOEL & COREY, 1932); tentatively

the Eagle Rest Peak area, San Emigdio region, southern Kern County, south-central California (LOEL & COREY, 1932); and tentatively the Vaqueros Creek area, Junipero Serra Peak region, Monterey County, north-central California (LOEL & COREY, 1932).

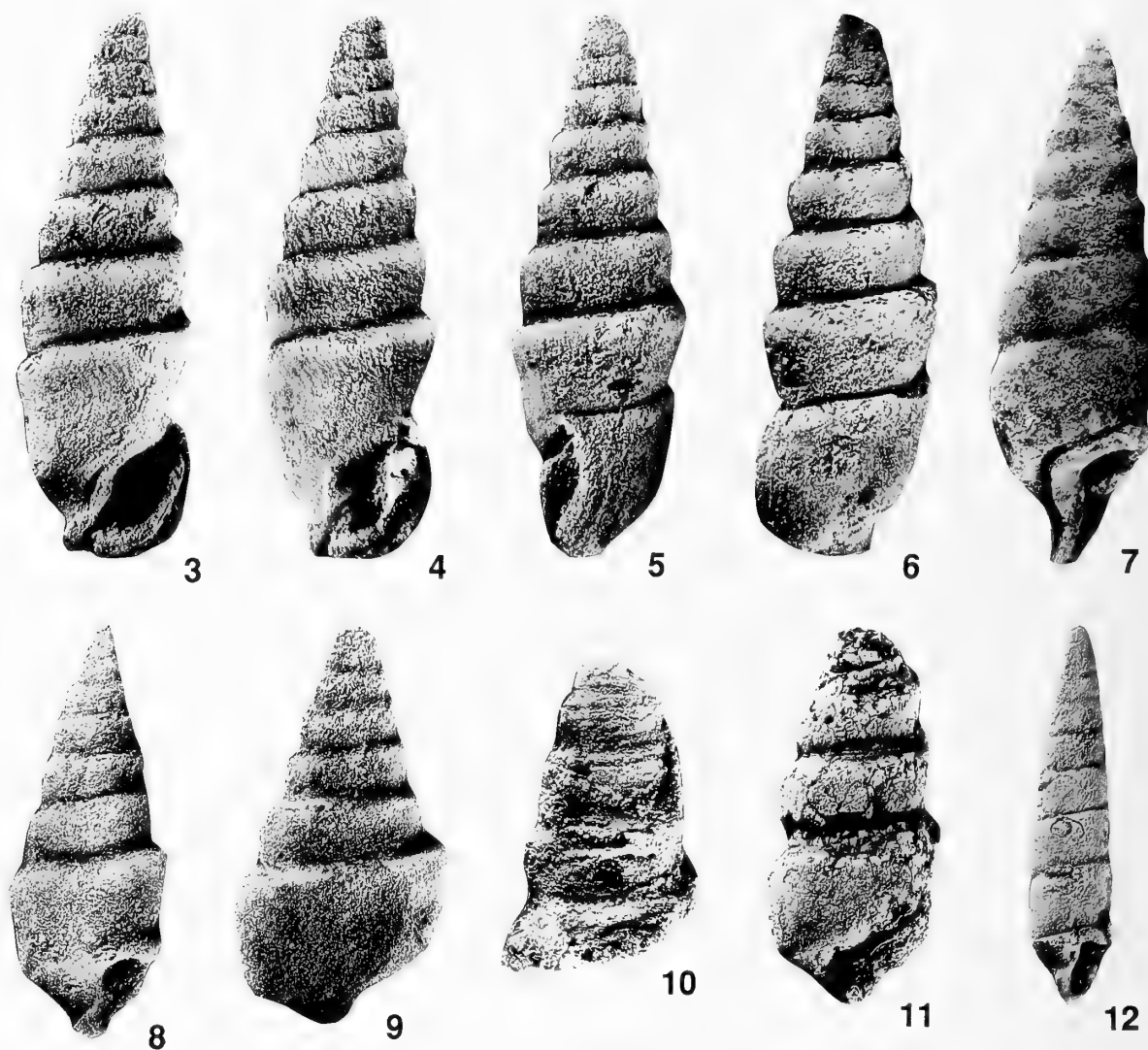
Remarks: A total of 340 specimens were seen during the course of this study. The holotype (Figures 3–6) is the best preserved specimen, but it is the only specimen that has a body whorl narrower than the penultimate whorl. The holotype also shows the central plait in the aperture better than any other specimen. Figure 4 illustrates the coincidence of this central plait with the columellar side of the anterior canal. The columellar callus is fairly well developed on the holotype, but the specimen illustrated in Figure 7 shows how pronounced this callus can be. The presence of a detached columellar callus helps to determine that this species is a cerithiid rather than a terebrid. In addition, the lack of a siphonal fasciole on *Clavocerithium (C.) santanum* further underscores that the species is not a terebrid, as all members of family Terebridae have a siphonal fasciole (BRATCHER & CERNOHORSKY, 1987).

The holotype is the only specimen that shows growth lines. These are readily discernible in Figures 3–5, and Figure 5 illustrates the sinuous outer lip. The whorls on the holotype are tabulate. A few specimens have convex whorls (Figure 7), and others are transitional (Figure 8) between convex whorls and prominently tabulate whorls (Figure 9). Variation in shell form is common in species of cerithiids (HOUBRICK, 1978; KAY, 1979), and well-illustrated examples are shown in HOUBRICK (1978:pls. 2, 13, 16, 94). His plate 94 shows examples of variation of shell form in *Clavocerithium*.

Nearly every observed specimen of *Clavocerithium (C.) santanum* is smooth over the entire shell. At locality LAC-MIP 7700, however, several partial specimens that consist of the middle part of the spire show faint traces of spiral ribbing on the spire whorls. One of these specimens (Figure 10) shows four spiral ribs. The spiral rib in the sutural area is, in most cases, the only spiral rib that is preserved (Figure 11). Abrasion of shell sculpture, therefore, is a major factor in the studied specimens. The abrasion may have taken place during post-mortem transport by waves and/or currents.

No specimens of *Clavocerithium (C.) santanum* were found that show any traces of spiral or axial ribbing on the exteriors of the more anterior spire whorls or on the body whorl. These whorls are judged to have originally been smooth. The presence of growth lines on the penultimate and body whorls of the holotype suggest that this particular specimen underwent minimal post-mortem transport, otherwise the growth lines would have been worn off. The whorls of this specimen show no spiral ribbing or other external ornamentation.

It is also possible that hermit crabs could have lived in the shells. Modern cerithiid shells commonly serve as homes for hermit crabs. For example, dead specimens of *Ceri-*



Explanation of Figures 3 to 12

Figures 3-12. *Clavocerithium (C.) santanum* (Loel & Corey, 1932). Figures 3-6: holotype UCMP 31608, locality UCMP 6128, apertural, oblique apertural, lateral, and abapertural views, $\times 3.8$; Figure 7: hypotype LACMIP 12103, locality LACMIP 7700, oblique apertural view, $\times 3.1$; Figure 8: hypotype LACMIP 12104, locality CSUN 1185, apertural view, $\times 2.6$; Figure 9: hypotype LACMIP 12105, locality CSUN 1185, abapertural view, $\times 3.3$; Figure 10: hypotype LACMIP 12106, locality LACMIP 7700, abapertural view of middle spire, $\times 3.1$; Figure 11: paratype UCMP 31611, locality UCMP A-252, apertural view, $\times 2.9$; Figure 12: hypotype LACMIP 12107, locality, LACMIP 7700, apertural view, $\times 3.5$.

thium stercusmuscarum in the northern Gulf of California are commonly inhabited by hermit crabs (HARTSHORNE *et al.*, 1987; FÜRISCH & FLESSA, 1987). Nearly all the specimens that I observed of this gastropod on the tidal sandflat at San Felipe were occupied by hermit crabs. Some of the abrasion of the shells of *Clavocerithium (C.) santanum* could have taken place during movements associated with the hermit crabs.

Only about 15% of the studied specimens of *Clavocerithium (C.) santanum* have retained their apertures, and

only a few of these specimens show the fragile outer lip, the very fragile detached columellar callus, and the central plait on the columella. These features, especially the central plait on the columella, could have been worn off if the shells served as homes for hermit crabs.

Most of the specimens of *Clavocerithium (C.) santanum* that are in the LACMIP collection from locality LACMIP 7700 consist only of the upper spire. Many of these are like other specimens of this species found elsewhere in that the upper spire whorls are straight sided for the first 3 to

6 mm in height and grade into tabulate whorls beyond that height. On a few specimens from locality 7700, however, the upper spire whorls remain straight sided for up to 15 mm in height (Figure 12), and the rest of the shell (presumably with tabulate whorls) is missing. Specimens with such long and slender upper spire whorls were detected only at this locality.

Previously, *Clavocerithium* (*Clavocerithium*) comprised only *C. (C.) lacazei* (COSSMANN, 1897:pl. 11, figs. 15, 17; 1898:15; 1920:94–95, pl. 3, figs. 24–25; WENZ 1940:762, fig. 2208; HOUBRICK, 1978:121, pl. 93, figs. 1, 2) from the upper? Eocene at Bois Gouët, Brittany, northwestern France. The exact age of these fossil beds has been much disputed, and assigned by various authors to either the middle Eocene or late Eocene (DAVIES, 1975:186).

On the basis of comparisons with several LACMIP specimens of *Clavocerithium* (*C.*) *lacazei* from Bois Gouët, as well as with the published illustrations of this species, *C. (C.) santanum* differs in having (1) a smaller shell, (2) whorls more tabulate (although a few specimens have convex whorls similar to those in *C. (C.) lacazei*, (3) four rather than 12 spiral ribs on middle of spire, (4) a detached columellar callus, (5) no axial ridges on upper whorls, and (6) a columellar callus that is not just restricted to the parietal area.

Clavocerithium (*Clavocerithium*) *santanum*, which is only the second species in the typical subgenus, is the first report of this subgenus in the New World, fossil or Recent, and the first early Miocene report.

Indocerithium Chavan, 1952, is the only other known subgenus of *Clavocerithium*. HOUBRICK (1975, 1978) reviewed *Indocerithium*, which is distinguished by an outer lip that extends one-third onto the previous whorl, and reported the subgenus to range from early Pliocene to Recent. Only three species are assigned to this subgenus, and two are extinct. All are from Indonesia and/or the Philippines and are associated with coral-reef biotopes.

The name *Clavocerithium* is a Latin neuter noun, and the species name *santana* must be changed to *santanum*.

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CSUN 159. SW $\frac{1}{4}$ of section 36, T6N, R22W, U.S. Geological Survey, 7.5-minute, Lion Canyon, California Quadrangle, 1943, upper Sespe Creek area, Ventura County, southern California (SQUIRES & FRITSCH, 1978:fig. 2B).

CSUN 401. SW $\frac{1}{4}$ of section 33, T6N, R21W, U.S. Geological Survey, 7.5-minute, Topatopa Mountains, California Quadrangle, 1943, upper Sespe Creek area, Ventura County, southern California (SQUIRES & FRITSCH, 1978:fig. 2C).

CSUN 428. In extreme NW corner of section 26, T6N, R22W, U.S. Geological Survey, 7.5-minute, Lion Canyon, California Quadrangle, 1943, upper Sespe Creek area, Ventura County, southern California (SQUIRES & FRITSCH, 1978:fig. 2B).

CSUN 555. NE $\frac{1}{4}$ of the SW $\frac{1}{4}$ of section 20, T3N, R 18W, U.S. Geological Survey, 7.5-minute, Simi, California Quadrangle, 1943, Big Mountain, north side of Simi Valley, Ventura County, southern California (BLUNDELL, 1981:pl. 1).

CSUN 1185. Along steep ridge, at elevation of 860 ft. (265 m), near head of Hicks Canyon, $37^{\circ}33'10''$ N and $118^{\circ}34'00''$ E (1000-meter Universal Transverse Mercator Grid, 1927 datum), U.S. Geological Survey, 7.5-minute, El Toro, California Quadrangle, 1968 (photorevised 1982), northern Santa Ana Mountains, Orange County, southern California (DANIEL, 1989: appendices B2 and C4).

LACMIP 7700. Cliff west of old adobe in SW part of Plano Trabuco, N40°W of old adobe, 34 m above stream bench in 1-m-thick bed of hard ledge-forming slimy sandstone, in places almost a coquina (LACMIP records), U.S. Geological Survey, 7.5-minute, Cañada Gobernadora, California Quadrangle, 1968 (photorevised 1988), southern end of northern Santa Ana Mountains, Orange County, southern California.

UCMP 6128. "At base of bluff, west of the S end of the remnant hill which is on the lower plain, west side of Plano Trabuco" (LOEL & COREY, 1932:57), U.S. Geological Survey, 7.5-minute, Cañada Gobernadora, California Quadrangle, 1968 (photorevised 1988), southern end of northern Santa Ana Mountains, Orange County, southern California.

UCMP A-253. "N side of first large gulch on E side of

Wiley Canyon, center of S side of section 36, T4N, R19W, lowest invertebrate fossiliferous bed (possibly estuarine deposition)" (LOEL & COREY, 1932:79), south side of Santa Clara River, Oak Ridge area, U.S. Geological Survey, 7.5-minute, Piru, California Quadrangle, 1952 (photorevised 1969), Ventura County, southern California.

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The Validity of *Chaetoderma montereyense* Heath Along with *Ch. argenteum* Heath (Mollusca: Caudofoveata)

by

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Abstract. The northeastern Pacific aplacophoran mollusk species *Chaetoderma argenteum*, *Ch. attenuatum*, and *Ch. montereyense* (Caudofoveata), diagnosed by HEATH (1911) and recently synonymized as a single species *Ch. argenteum* Heath, are reexamined. Detailed analysis of the type material reveals (1) that Heath's description of *Ch. attenuatum* refers to a specimen of *Ch. montereyense*, and (2) that *Ch. attenuatum* is anatomically (pericardium and other characters) and geographically (Alexander Archipelago, south Alaska) identical with *Ch. argenteum* only. Thus, *Ch. attenuatum* can be synonymized with *Ch. argenteum*, whereas *Ch. montereyense* (off Santa Barbara, California to Vancouver, B.C.) is to be maintained as a valid species.

INTRODUCTION

HAROLD HEATH (1911) described the aplacophoran Mollusca ("Solenogastres")—i.e., the Solenogastres proper (= former Neomeniomorpha) as well as the separated Caudofoveata (= former Chaetodermomorpha)—of an expedition in 1899–1900 to the tropical Pacific. Whereas the Solenogastres proper are adequately presented, the descriptions of the Caudofoveata (viz. *Chaetoderma* and *Limifossor*) are in part scanty. This has caused some difficulties in specific identification (cf. STORK, 1941:55; SALVINI-PLAWEN, 1972:228, 1992; SCHELTEMA *et al.*, 1991), especially concerning the species diagnosed by Heath as *Chaetoderma attenuatum* and *Ch. montereyense*¹.

In their recent paper, SCHELTEMA *et al.* (1991) considered specific identity not only of those two nominal species (not really different according to Heath; see also STORK, 1941:55), but they declared both to be junior synonyms of *Chaetoderma argenteum* HEATH, 1911. With respect to *Ch. argenteum*, however, there are differences described by Heath. Within the general organization of the Caudofoveata (see SALVINI-PLAWEN, 1985, for a detailed account),

the present contribution points out these differences based on an anatomical analysis and evaluates them with respect to conspecificity.

THE MATERIAL CONCERNED

(1) H. Heath described the new species *Chaetoderma argentea* (correctly: *argenteum*) on the basis of a single, 24-mm-long specimen. This was collected at Albatross Sta. 4231 in 82–113 fms (150–207 m) from the Alexander Archipelago in south Alaska, near Naha Bay in the Behm Canal (55°59'N, 131°17'W; HEATH, 1911:9, 62). This type is deposited in the California Academy of Sciences as a slide series CAS no. 190 (STASEK, 1966:2).

(2) The description of *Chaetoderma attenuata* (correctly: *attenuatum*), likewise from the Alexander Archipelago in south Alaska, by HEATH (1911:9, 43, 55–59) was based on a total of eight individuals (not "16" specimens as incorrectly indicated by STASEK, 1966:2) measuring up to 61 mm in length. Five specimens came from Albatross Sta. 4250 (Simonof Island, opposite the mouth of the Stikine River, about 56°42'N, 132°25'W, at 61–66 fms = 87–94 m depth), one individual from Sta. 4244 (Kasaan Bay of Clarence Strait, at the eastern coast of Prince of Wales Island, 55°30'N, 132°25'W, at 50–54 fms = 91.5–98 m) and two specimens from the geographically more distant Sta. 4252 (Stephens Passage at 198–201 fms = 360–368 m depth). HEATH definitely speaks of a type specimen (1911:55) which, *bona fide* in agreement with STASEK (1966:

¹ The generic name *Chaetoderma* is of neuter gender (see also Opinion 764 in the *Bulletin of Zoological Nomenclature* 23(1):22 (1966)). Consequently, as already done in SALVINI-PLAWEN 1972:380, all species need neuter endings (in contrast to HEATH's (1911) original spellings): Article 34b of the ICZN.

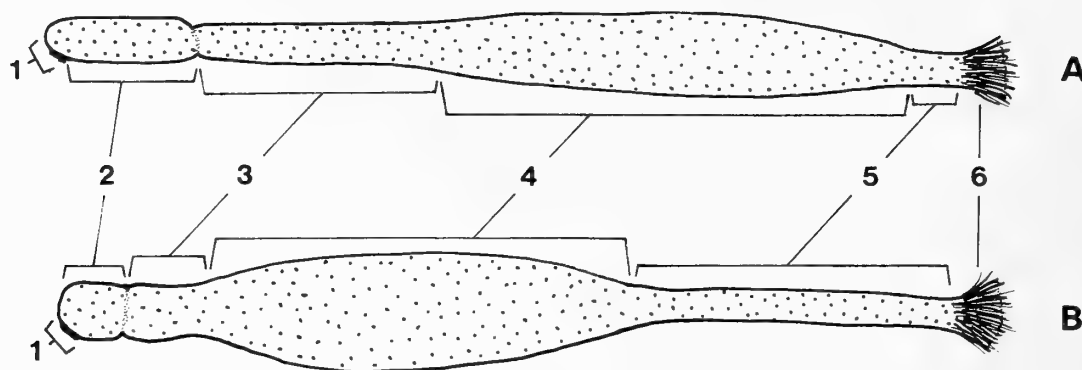


Figure 1

Body regions in the Caudoveata-Chaetodermatidae. 1, peribuccal region; 2, region of foregut; 3, region of midgut (anterior trunk); 4, region of midgut sac (posterior trunk); 5, prepallial region (of gonopericardial ducts); 6, region of pallial cavity (after SALVINI-PLAWEN, 1975). The *Chaetoderma* species treated here correspond to the regionation in "A" (see also SCHELTEMA *et al.*, 1991:fig. 1).

2), is identical with the sectioned animal CAS no. 191. Other material is kept as paratypes by the MCZ at Harvard University (see also SCHELTEMA *et al.*, 1991:table 1). At present they include four specimens from Sta. 4250, the single individual from Sta. 4244, and the two specimens from Sta. 4252. The individual from Sta. 4244 is preserved together with two specimens from Sta. 4250 (one individual without a posterior body portion and two specimens lacking the foregut region; one animal of this mixed sample, a fragment of 40 mm, has been used here to prepare serial sections of the posterior body, see below). Thus, seven individuals (in part being incomplete) are retained in alcohol, and the eighth specimen had been used for the series section (CAS no. 191).

(3) A third *Chaetoderma* species from the Alexander Archipelago had been described by HEATH (1911:9, 43, 59–61) as *Ch. erudita* (correctly: *eruditum*). Ten specimens of up to 27 mm in length were taken in the Lynn Canal at 300–313 fms (549–573 m) depth (Albatross Sta. 4258) and 41 individuals came from the Chatham Strait at 282–293 fms (516–536 m) depth (Sta. 4264). This material (paratypes; holotype = ?) is held in the MCZ at Harvard University.

(4) Among the species described by Heath from off California, *Chaetoderma montereyensis* (correctly: *montereyense*) was represented by 181 specimens. They measure up to 45 mm in length and stem from eight stations (nos. 4485, 4508, 4510, 4522, 4523, 4524, 4525, 4526) at 39–356 fms (71–642 m) depth in Monterey Bay (HEATH 1911: 9, 43, 61; supplemented in SCHELTEMA *et al.*, 1991:table 1). No type was designated by HEATH (1911), but one of the above 181 syntypes is maintained as a series section on slides (CAS no. 194). This is herein designated as the lectotype, rather than a syntype (STASEK, 1966:3) or the holotype (SCHELTEMA *et al.*, 1991:table 1).

COMPARATIVE ANALYSIS

As was the case with several other descriptions of Caudoveata by HEATH (1911), the diagnostic characters of the four nominal species in question are also only scantily elaborated. Generally, a detailed analysis of the sequence of the mantle scales along the regionated body (Figure 1) will reveal specific differences (cf. SALVINI-PLAWEN, 1978); in the present case, no such detailed representation of the spicules exists. The illustration of the aragonitic body scales by HEATH (1911:pl. 37) is similar for all *Chaetoderma* species and is thus not truly informative. SCHELTEMA *et al.* (1991:fig. 3A) provide camera lucida drawings of *Ch. argenteum* spicules that are very similar to those of *Ch. montereyense*. On the other hand, the present author also examined the mantle scales of four paratypes of *Ch. eruditum* Heath (HEATH, 1911:Stat. 4258, 4264); the bent spicules in the midgut region (cf. also HEATH, 1911:pl. 37, fig. 15) resemble those of the above-named species. Other spicules of *Ch. eruditum*, however, are distinctly different (*e.g.*, in the region of the midgut sac: Figure 2). Thus, *Chaetoderma eruditum* Heath is well-diagnosed by its spicules alone and can be excluded from the present discussion.

In May 1966, several *Chaetoderma* samples from Puget Sound were submitted by K. Banse (University of Washington, Seattle) to the present author. Based on the description by HEATH (1911), several specimens represent either *Chaetoderma montereyense* or *Ch. attenuatum*. The body cover (mantle scales) is almost identical in paratypes of both nominal species (see Figures 3, 4). Based on the mantle scales, three additional specimens from Puget Sound, Seattle, Washington sent in 1979 to the present author by F. Nichols (U.S. Geological Survey, Menlo Park, California), were likewise identified (February, 1980) as *Ch.*

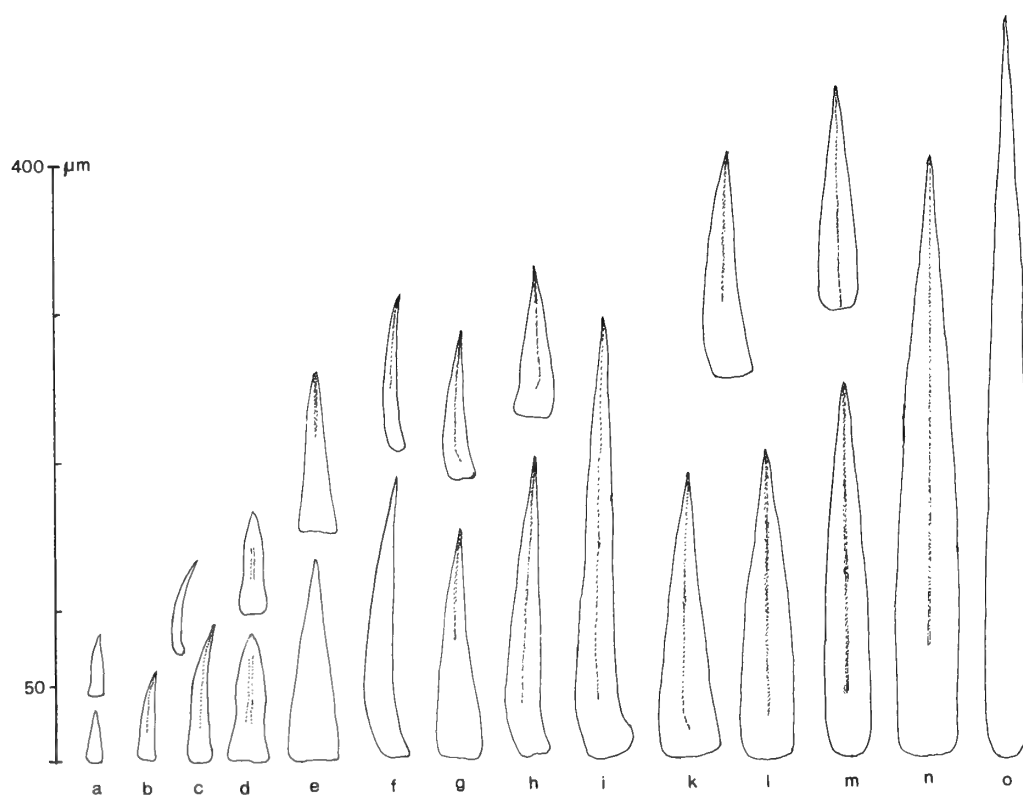


Figure 2

Sequence of mantle scales in *Chaetoderma eruditum* Heath (paratype Sta. 4258). a-d, foregut region; e-i, midgut region; k-m, region of midgut sac; n-o, prepallial and pallial regions.

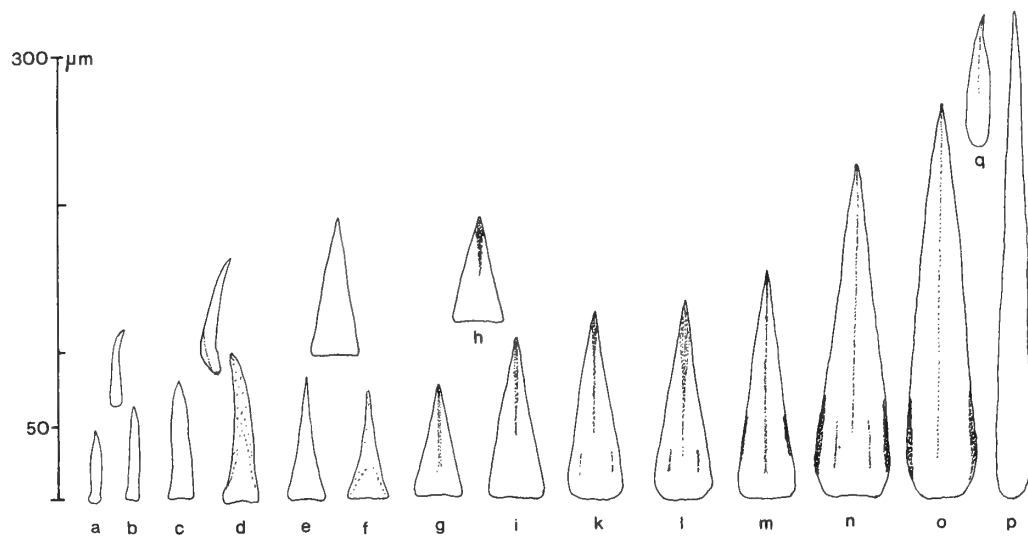


Figure 3

Sequence of mantle scales in *Chaetoderma montereyense* Heath (paratype Sta. 4526). a-b, foregut region; c-i, midgut region; k-n, region of midgut gland; o-p, prepallial and pallial regions; q, bordering the dorsoterminal sense organ.

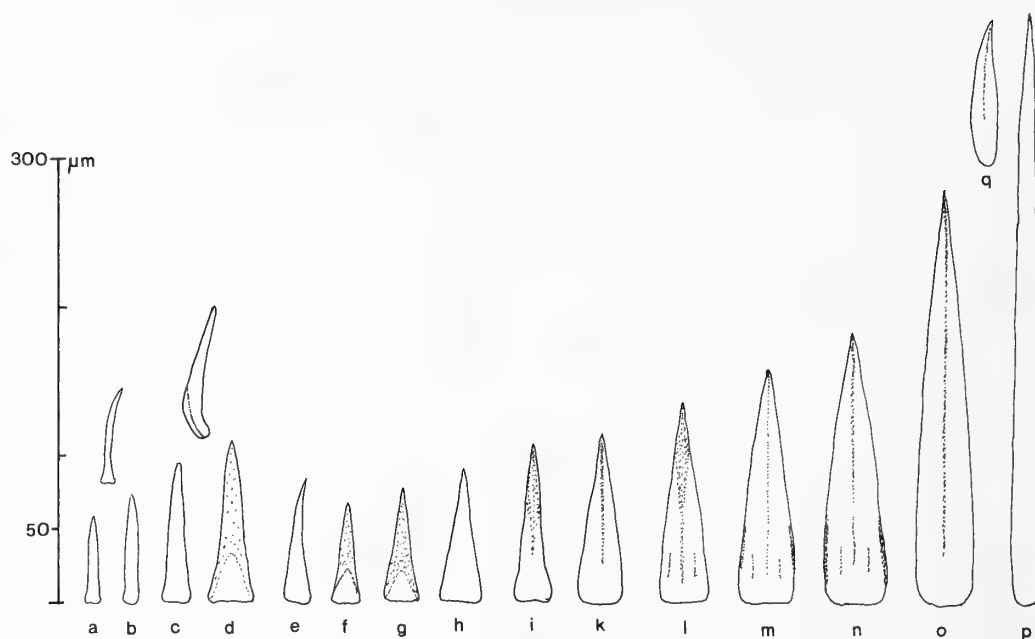


Figure 4

Sequence of mantle scales in *Chaetoderma attenuatum* Heath (paratype Sta. 4250). a–b, foregut region; c–i, midgut region; k–n, region of midgut sac; o–p, preapallial and pallial regions; q, bordering the dorsoterminal sense organ.

montereyense. SCHELTEMA *et al.* (1991) presented recent findings of *Chaetoderma* material from Point Conception, California, to Vancouver Island, British Columbia (see also BUCKLAND-NICKS & CHIA, 1989). The animals belong to *Ch. montereyense* Heath (as already hinted by the present author to Buckland-Nicks in a letter on 26 January 1990), a species which SCHELTEMA *et al.* (1991), mainly due to the similarity of the mantle scales, synonymized not only with *Ch. attenuatum* but also with *Ch. argenteum*. Contrary to the opinion of SCHELTEMA *et al.* (1991:208) that HEATH (1911) "did not differentiate *C. argenteum*, *C. attenuata*, and *C. montereyensis* either by written description or by illustration," there are described differences as concerns *Ch. argenteum* (cf. HEATH, 1911; see below). Thus, a re-examination of the series-sectioned type material of the three nominal species was undertaken in order to clarify the discrepancies between Heath's description and the above synonymization. In addition, Dr. K. Boss (Curator at the MCZ, Harvard) permitted the posterior end of one *Ch. attenuatum* paratypes to be series sectioned.

The detailed anatomical comparison of all three nominal species revealed a far-reaching identity in internal organization (for exceptions, see below). Beside the general similarity of the mantle scales (Figures 3, 4; see also SCHELTEMA *et al.*, 1991), they also share the pedal shield with an anterior oral cleft (according to the type series of *Chaetoderma argenteum*; HEATH, 1911:56 and personal observation for *Ch. attenuatum*; personal observation and SCHELTEMA *et al.*, 1991, for *Ch. montereyense*, in contrast to HEATH, 1911:1.4, figs. 14, 17). The foregut with its

glands, as well as the radula apparatus, coincide (in *Ch. montereyense* the latter is not "exceptionally heavy and powerful" as described by HEATH, 1911:62, but merely in a different state of contraction). The different size of the radular basal cone may reflect relative body size ($300 \times 100 \mu\text{m}$ in *Ch. argenteum*, up to $500 \times 200 \mu\text{m}$ in *Ch. attenuatum*, and up to $500 \times 175 \mu\text{m}$ in *Ch. montereyense*). There are six pairs of precerebral ganglia and a dorso-posterior *lobus impar* joining the cerebral ganglia (SALVINI-PLAWEN, 1972:298); the posterior nervous system is almost identical, including the ventral ctenidial nerves (= the so-called subrectal commissure of WIREN, 1892:taf. VII, fig. 3) emerging ventrally from the suprarectal ganglionic mass. All three nominal species show a strong, more or less separated lateral muscle bundle along both sides of the foregut-anterior midgut. For comparison, this paired bundle represents a specific character of *Ch. nitidulum* Loven, in contrast to *Ch. canadense* Nierstrasz (where it is missing; cf. SALVINI-PLAWEN, 1988:308).

In general, two pairs of retractors from the efferent side of the ctenidia (posteriodorsal and anteriodorsal bundles which mostly pass the pericardium) and two pairs of afferent ctenidial retractors (lateral and ventral bundles) exist. They show individual variability in strength, but the ventral retractors are the strongest; in *Scutopus ventrolineatus* Salvini-Plawen the latter continue into the *m. longitudinalis* and enable the body to roll up. Incomplete or complete subdivision may result in five pairs (e.g., in *S. ventrolineatus*; cf. also WIREN, 1892; see Figure 5 herein) or even six pairs (e.g., in *Prochaetoderma californicum*

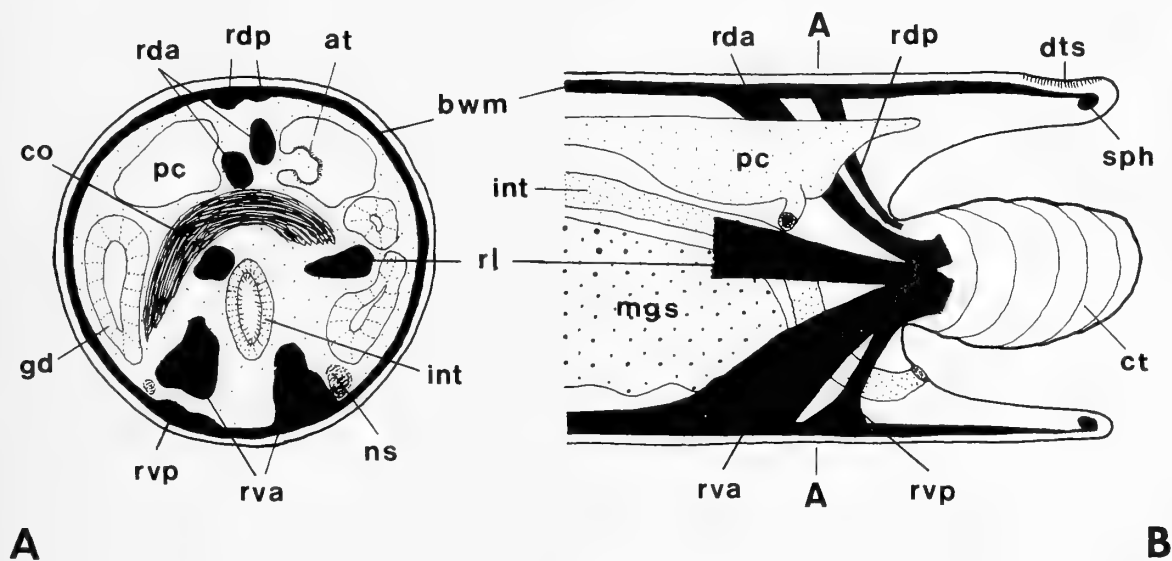


Figure 5

Arrangement of musculature in the posterior body of Caudofoveata. A. Cross section along line A-A in B. B. Lateral projection. at, atrium of heart; bwm, body wall musculature; co, ganglionic suprarectal commissure; ct, ctenidium; dts, terminal sense organ; gd, glandular duct; int, intestine; mgs, midgut sac; ns, fused lateral/ventral nerve cord; pc, pericardium; rda, anteriodorsal retractor; rdp, posteriodorsal retractor; rl, lateral retractor; rva, anterioventral retractor; rvp, posteroventral retractor; sph, terminal sphincter of the pallial cavity.

Schwabl; cf. also SCHWABL, 1963). In all three nominal species treated here, four pairs of ctenidial retractors are present as in *Chaetoderma canadense* or *Ch. intermedium* Knipowitsch (personal observation). The ventral retractors show a posterior portion which, however, is not separated; the posteriodorsal retractors insert at the basi-ctenidial wall of the mantle cavity.

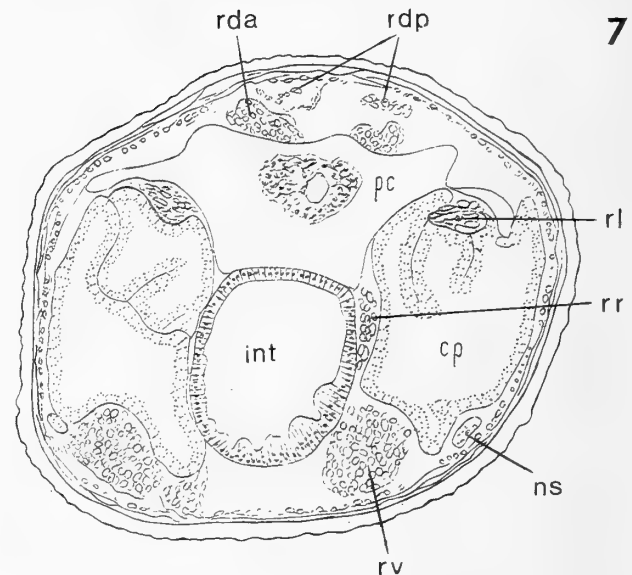
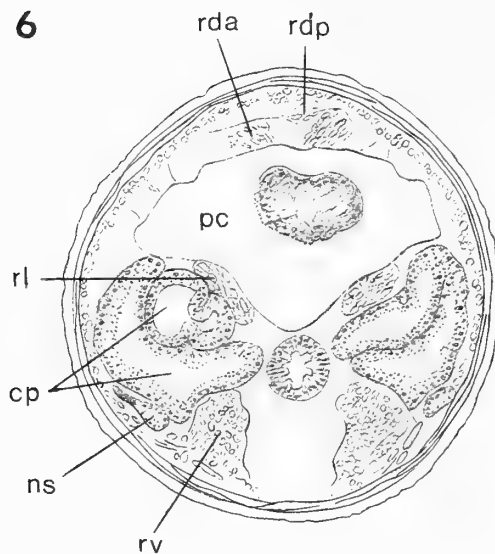
The heart runs freely within the pericardium and bears, at the anterior end of the latter, a middorsal opening. Anterior to the aortal bulbus, the vessel continues as an aorta within the lumen of the gonopericardioduct and within the posterior portion of the fused gonad; the gonopericardioduct itself is unpaired, laterally and/or ventrally ciliated and has sporadic ventral and/or dorsal connecting suspensions of the aorta. The pericardial outlets, composed on each side of two sections, viz. a ciliated pericardioduct and a spacious glandular duct, are of identical outline in the three nominal species: the pericardioducts are very short and open directly into the upper dorsoposterior limb of the U-shaped glandular ducts, as correctly described and illustrated by HEATH (1911) for *Ch. argenteum* only (see Figure 8).

Despite all these coincidences, however, distinct differences exist:

- (1) In *Chaetoderma argenteum*, (a) the spicules preserved with the type CAS no. 190 (slide 92) fit into the configurations of the elements in the two other nominal species without marked differences (cf. SCHELTEMA *et al.*, 1991:fig. 3). Due to the single, sectioned specimen, no further reexamination is possible. (b) As is illus-

trated by HEATH (1911:pl. 26, fig. 5; pl. 36, fig. 1), there is no extension of the pericardium beyond the beginning of the pallial cavity. (c) The ventral, lateral, and anteriodorsal ctenidial retractors are paired and of usual elaboration. (d) The posteriodorsal ctenidial retractors represent an unpaired bundle (see Figure 6) that splits only upon reaching the dorsal body wall. (e) The buccal connective branches off at each side of the common trunk (of connectives from the cerebral ganglion) fairly early at a distance of 120 μm . (f) The recorded locality is the Behm Canal in the southwestern Alexander Archipelago (south Alaska).

- (2) In *Chaetoderma montereyense*, (a) the spicules (g-i) in Figure 3 (= scales '4' in SCHELTEMA *et al.*, 1991:fig. 3D) appear to be dominant in the posterior midgut region. (b) As described by HEATH (1911:62), the "pericardium is a comparatively spacious chamber," extending behind the heart broadly backward some distance over the mantle cavity; this is also correctly illustrated (HEATH, 1911:pl. 27, fig. 9). (c) Although the ventral, lateral, and anteriodorsal pairs of ctenidial retractors are elaborated as usual, there is an additional (lateral) bundle on the right side (Figure 7 rr); it originates together with the right lateral retractor and inserts at the hindgut as illustrated by Heath (see Figure 7, herein). (d) The posteriodorsal ctenidial retractors begin as a paired bundle which fuses at the level of the pericardium (cf. HEATH, 1911:pl. 27, fig. 8) and splits again upon reaching the middorsal body wall (Figure 7). (e) The buccal connective splits off the common trunk at a distance of 200 μm .



Explanation of Figures 6 and 7

Figure 6. Cross section through heart and glandular ducts of *Chaetoderma argenteum*, taken from HEATH (1911:pl. 26, fig. 3). cp, glandular duct; ns, fused lateral/ventral nerve cord; pc, pericardium; rda and rdp, anteriodorsal and posteriodorsal ctenidial retractors; rl, lateral ctenidial retractor; rv, ventral ctenidial retractor.

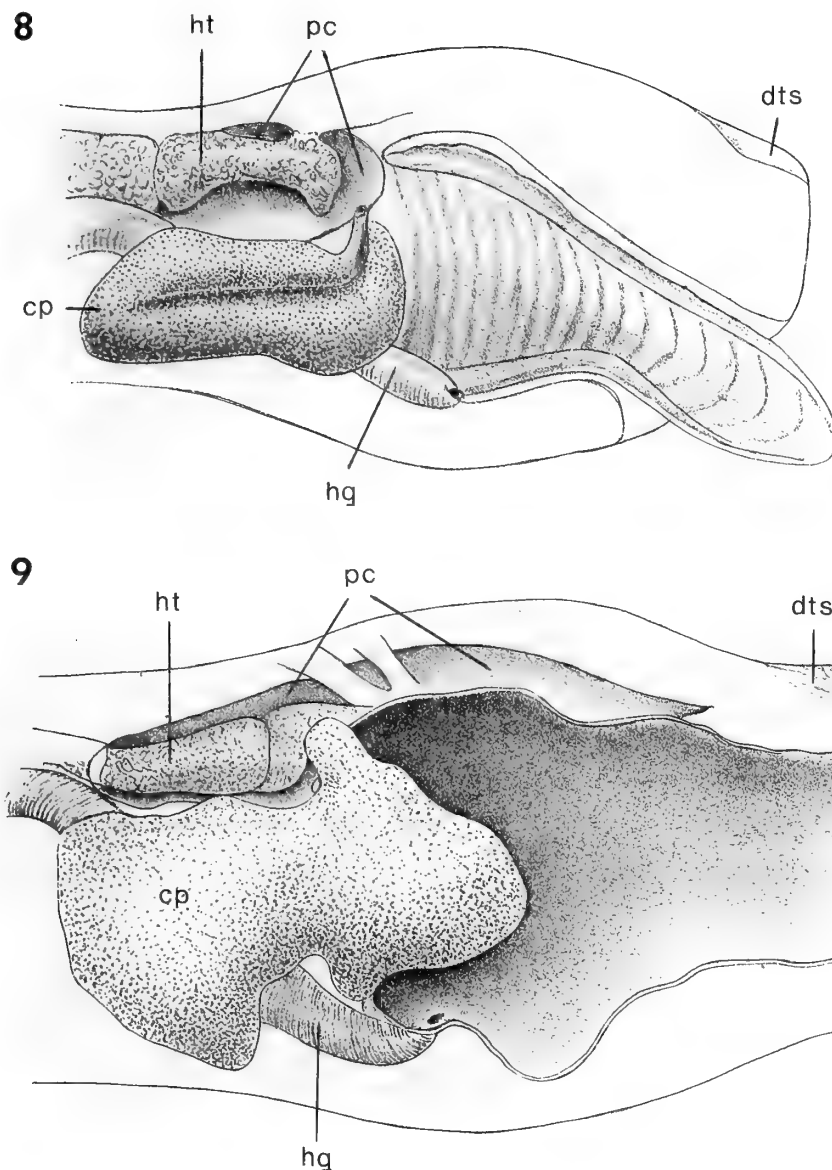
Figure 7. Cross section through heart and glandular ducts of *Chaetoderma montereyense*, taken from HEATH (1911:pl. 27, fig. 2). cp, glandular duct; int, intestine; ns, fused lateral/ventral nerve cord; pc, pericardium; rda and rdp, anteriodorsal and posteriodorsal ctenidial retractors; rl, lateral ctenidial retractor; rr, ctenidial retractor to hindgut; rv, ventral ctenidial retractor.

These characters of the lectotype (a female) correspond exactly with the sectioned Puget Sound, Seattle (1966) specimen (a male). The characters are unrelated to different body sizes, for example with respect to the length of the common trunk of connectives. Some scales are present, however, which correspond to the spicule 'i' in Figure 4, and the asymmetrical muscle bundle at the hindgut is less prominent. (f) The geographical distribution thus clearly includes Monterey Bay, California (type material), and Puget Sound, Washington, but probably ranges from Point Conception, California, to Rainy Bay, off SW Vancouver Island, southern British Columbia (BUCKLAND-NICKS & CHIA, 1989; SCHELTEMA *et al.*, 1991).

- (3) The description of *Chaetoderma attenuatum* by HEATH (1911:55–59) largely corresponds to that of *Ch. montereyense* (STORK, 1941:55; SALVINI-PLAWEN, 1972:228; SCHELTEMA *et al.*, 1991). The coincidence also includes the pericardium, which "is of unusual size, extending behind the heart nearly to the posterior end of the body" (HEATH, 1911:58, also pl. 25, fig. 5, and pl. 36, fig. 2). This specimen is a female as evidenced by the mucous tracts ("glandular epithelium") in the ventral mantle cavity (HEATH, 1911:58, and drawn in fig. 5 of pl. 25).

This description, however, does *not* correspond to the type material! (a) Spicules of paratypes show differences in their dominance in the posterior midgut

region (Figure 4g–i) when compared with *Chaetoderma montereyense*. The sole series-sectioned individual of *Ch. attenuatum* (holotype, CAS no. 191) is a male and its anatomy points to *Ch. argenteum*. (b) The pericardium does not extend beyond the beginning of the mantle cavity. (c) Among the ctenidial retractors there is no particular retractor to the hindgut (merely the left lateral retractor is bipartite). (d) The posteriodorsal ctenidial retractor is largely unpaired. (e) The buccal connective emerges after a short distance of 80–120 μ m. And (f) the animals originate from the Alexander Archipelago, south Alaska. Yet, the posterior-most body is ventrally bent and hence obliquely sectioned (and in no way corresponds to figs. 4, 5, and 8 of pl. 25 in HEATH, 1911); in addition, this part is in poor histological condition. Consequently the posterior body of a paratype of the above-mentioned mixed sample had been series sectioned for certainty: this specimen either originated from the type locality (Sta. 4250, off Simonof Island) or it represents the single individual from the sample Sta. 4244 (Kasaan Bay of Clarence Strait), which is closest to the type locality of *Ch. argenteum*. Its anatomy (a male in moderate histological condition) likewise fully coincides with the specific characters of *Ch. argenteum* (pericardium, ctenidial retractors) but not with *Ch. montereyense*. The difference in body size, 24 mm *Ch. argenteum* versus more



Explanation of Figures 8 and 9

Figure 8. Reconstruction of posterior end of *Chaetoderma argenteum*, taken from HEATH (1911:pl. 36, fig. 1). cp, glandular duct; dts, terminal sense organ; hg, hindgut; ht, heart; pc, pericardium.

Figure 9. Reconstruction of posterior end (without ctenidium) of *Chaetoderma dict. "attenuatum,"* taken from HEATH (1911:pl. 36, fig. 2). cp, glandular duct; dts, terminal sense organ; hg, hindgut; ht, heart; pc, pericardium.

than 40 mm of the sectioned *Ch. attenuatum* paratype, is of no relevance for the anatomical configuration.

DISCUSSION

The Caudofoveata are animals having a fairly uniform organization (see SALVINI-PLAWEN, 1985 for a general outline), and classification at the species level may cause difficulties. Generally, differences in the sequence of the mantle scales (size, outline, structure) are sufficient to de-

fine a species. In cases where such differences may not be distinct enough, additional characters are needed. This is true for the chaetodermatids *Falcidens chistos* Scheltema (1989) and *F. targotegulatus* Salvini-Plawen (1992), the latter being also defined by its perioral pedal shield. Similarly, *Chaetoderma canadense* Nierstrasz and *Ch. nitidulum* Loven are distinguished by scales, the radula apparatus, and the presence of the paired lateral muscles bundle along the anterior midgut (SALVINI-PLAWEN, 1975:43; 1978;

1988:308 *versus* SCHELTEMA *et al.*, 1991:212). In addition, *Ch. nitidulum* elaborates a (proximally paired) posteriodorsal ctenidial retractor, which splits into four bundles (WIREN, 1892, and personal observations), whereas the posteriodorsal retractor in *Ch. canadense* is unpaired-fused and does not split before reaching the middorsal body wall (personal observations); in *Ch. intermedium* Knipowitsch this retractor emerges paired, but continues fused-unpaired and enters the body wall musculature again as a paired bundle.

In contrast to the almost identical scales of *Chaetoderma argenteum* and *Ch. montereyense*, the listed differences are of species-specific significance. Especially pericardium and ctenidial retractor features do not allow postulation of conspecificity between *Ch. montereyense* and *Ch. argenteum*. A better knowledge of the geographical distribution of these two species (inshore and offshore regions) off British Columbia, north to Vancouver, may shed more light on this matter. The nominal species *Ch. attenuatum* represents an "accident" or at least a mistake: since the sole sectioned specimen (= type) does not correspond to Heath's own description and drawings, he obviously confused or mixed up series-sectioned material in the Hopkins Laboratory² and described a *Ch. montereyense* specimen as *Ch. attenuatum*.

Consequently, the synonymization of *Chaetoderma attenuatum* with *Ch. montereyense* (as could be suggested by Heath's descriptions; see STORK, 1941:55), as well as of both these nominal species with *Ch. argenteum* (as done by SCHELTEMA *et al.*, 1991) is rejected with respect to anatomical differences. The distinct specific validity of *Ch. montereyense* Heath is maintained along with *Ch. argenteum* Heath; *Ch. attenuatum* Heath, however, is put into synonymy with *Ch. argenteum*.

² The material described by Heath basically belonged to the MCZ at Harvard University (cf. HEATH 1911:9). The material to be elaborated (mainly serial sections) was taken by Heath to the Hopkins Laboratory, Stanford University, California. After Heath was dead, most of his collection was given by his son to the Hopkins Laboratory; other material was discarded (personal communication, K. Boss). Some slides were then taken by P. Riser from Hopkins Laboratory to Northeastern University, Nahant, Massachusetts, and later forwarded to Harvard MCZ again (personal communication, K. Boss). In 1965, the slide material

at the Hopkins Laboratory was transferred to the California Academy of Sciences, from which STASEK (1966:1) listed the type specimens.

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An Empirical Evaluation of Various Techniques for Anesthetization and Tissue Fixation of Freshwater Unionoida (Mollusca: Bivalvia), with a Brief History of Experimentation in Molluscan Anesthetization

by

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Abstract. The successful anesthetization and fixation of freshwater bivalves is necessary for study of their anatomy and fine structure. This need is further underscored by the possible elimination of many of the indigenous North American unionacean fauna by the introduced zebra mussel *Dreissena polymorpha* (Pallas, 1771). A number of techniques are empirically tested. The results of some of the various methodologies are compared using scanning electron microscopy. Optimal methods are suggested, with an additional primary treatment recommended for those genera that are difficult to anesthetize successfully. The literature on molluscan anesthetization methodology, exclusive of Cephalopoda, is reviewed.

INTRODUCTION

The preservation of the soft anatomy of mollusks is essential to taxonomists for correct systematic placement of the more problematic molluscan taxa. This is especially true in non-marine mollusks in which convergence of shell morphologies is exhibited in a number of rapidly evolving genera of the freshwater bivalve families Unionidae and Mycetopodidae. The need for careful preservation methodology of soft anatomy has been documented for the preservation of land snails by EMBERTON (1989) and is further accentuated by the work of DAVIS *et al.* (1981), who demonstrated convergence in shell morphologies among genetically distinct species of the bivalve genus *Elliptio*.

Students of the comparative anatomy of freshwater bivalve unionid mollusks should anesthetize specimens to relax the tissues to their natural appearance, and follow up by proper tissue fixation with buffered glutaraldehyde in order to preserve lifelike anatomical specimens of fresh-

water bivalves. The techniques of anesthetization and tissue fixation recommended here are highly useful in the lifelike preservation of unionid bivalves for use in anatomical investigations of both gross comparative anatomy and for the exploration and documentation of microanatomy via scanning electron microscopy. Further tissue fixation using osmium tetroxide is required should anatomical analysis via transmission electron microscopy be desired. However, these techniques are not appropriate for molecular genetics studies requiring mitochondrial DNA extraction.

There is some degree of urgency in adopting effective techniques. Since its introduction into the lower Great Lakes in 1985, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) has spread rapidly and has been predicted to invade nearly all of the freshwater systems of North America (STRAYER, 1991). HUNTER & BAILEY (1992) predicted that the effect of the zebra mussel upon freshwater unionids may possibly result in the virtual elimination of the indigenous North American unionid fauna.

The history of experimentation with the anesthetization of various molluscan taxa, exclusive of the Cephalopoda,

¹ Published posthumously. Proofs read by Dr. James H. McLean.

documents the use of a wide array of chemicals. Much of the previous experimentation on the anesthetization of mollusks has involved freshwater gastropods, largely as a result of parasitologically orientated research. Only one study has been undertaken to date on freshwater unionid bivalve taxa (FLORKIN, 1941).

Finally, any person who intends to experiment with the chemical anesthetization of mollusks first must consult the appropriate MSDS chemical data sheets for precautionary safety and health recommendations, use a chemical fume hood and chemical fume safety masks, and wear appropriate chemical hazard apparel. If experimentation in molluscan anesthetization with controlled substances such as sodium pentobarbital is desired, the investigator must obtain legal federal permits for such substances. The author is not responsible for any health problems of anyone who experiments with the substances and procedures described herein.

MATERIALS AND METHODS

Here I compare the anesthetic properties of nembutal, chloral hydrate, and 3-aminobenzoic acid ethyl ester, all followed by second stage treatment with 2-phenoxyethanol. I examine the results of killing of unionids in 70% ethanol, as well as 20% glutaraldehyde. I also compare the results of three anesthetization procedures in unfixed specimens that have been placed directly into 70% ethanol, with specimens that have been properly fixed with buffered glutaraldehyde following anesthetization. Finally, I compare the results of fixation of specimens following anesthetization and placement directly into 70% ethanol.

Specimens of two species of the genus *Elliptio* were collected by W. Henry McCullagh, from two localities on the St. Johns River system, Florida. Specimens were packed in ziplock plastic bags and shipped on synthetic ice overnight to the Los Angeles County Museum of Natural History (= LACM) where they were subjected to a variety of preservation methodologies. *Elliptio icterina* (Conrad, 1834) s.l. [population described as *Unio occulta* (Lea, 1843) and subsequently synonymized under *Elliptio icterina* s.l. by JOHNSON (1970)] was collected in 0.5 to 1 m in depth from mud and detritus in Middle Haw Creek, a tributary of Crescent Lake, approximately 13 km southwest of Bunnell, Flagler Co., Florida (29°23.2'N, 81°21.3'W), 18 July 1992 (WHM 575 = LACM 92-49). *Elliptio dariensis* (Lea, 1842) s.l. [population described as *Unio monroensis* (Lea, 1843) and subsequently synonymized under *Elliptio dariensis* s.l. by JOHNSON (1970)] was collected in 1 m depth from a sandy mud substrate in the main stem of Black Creek at the public boat ramp at Middleberg, Clay Co., Florida (30°04.58'N, 81°50.58'W), 19 July 1992 (WHM 577 = LACM 92-50). Additional specimens of *Lampsilis* sp. (possibly a new species; to be resolved in later systematic studies) were collected from the upper Alabama River system by Paul Hartfield, 25 June 1992 (PDH 92-32 = LACM 92-71.3). *Lampsilis* sp. were anesthetized and fixed via the primary methodology recommended herein and

subjected to intensive investigation of microanatomy via SEM. The results of that analysis are to be included in a broader paper dealing with the systematics of lampsilines; however, I document here the results of correct anesthetization and fixation procedure with respect to the cilia of the ctenidia, particularly the lifelike position of the latero-frontal cilia.

DAVIS *et al.* (1981) have shown that the *Elliptio icterina* group exhibits high genetic heterozygosity and numerous polymorphic loci, indicating that many of the 46 junior synonyms listed by JOHNSON (1970) deserve further study. *Elliptio dariensis* s.l. (Lea, 1842) is listed by JOHNSON (1972) as having only three junior synonyms. "*Unio*" *monroensis* (Lea, 1843) differs in shell morphology and type localities from *Elliptio dariensis* s.s. The Altamaha River is the type locality of *E. dariensis* s.s., whereas the St. Johns River system is the type locality of "*Unio*" *monroensis*. "*Unio*" *occulta* (Lea, 1843), and "*Unio*" *monroensis* (Lea, 1843) may indeed be valid species of the genus *Elliptio*, and it may prove useful to document the anatomies of these two taxa for use by future systematists; however, it is not within the purview of this paper to present resolutions of taxonomic problems.

Two primitive preservation methods, devoid of anesthesia, were compared: two specimens (LACM 92-49.3) of *Elliptio icterina* s.l. [= *Unio occulta*] were pegged open and placed alive into 70% ethanol (see Table 1), and two additional specimens (LACM 92-49.4) were pegged open and placed alive into 20% glutaraldehyde (see Table 1). The use of formalin as a fixative was avoided, as even buffered formalin can destroy the chitinous rods of the demibranchs (personal observation) and render tissue hard, brittle, and useless for dissection within two to four years in land snails (SOLEM *et al.*, 1981).

Three primary, or first stage, anesthetics were used experimentally on specimens of both *Elliptio icterina* s.l. [= "*Unio*" *occulta*] and *Elliptio dariensis* s.l. [= "*Unio*" *monroensis*]: (1) 3-aminobenzoic acid ethyl ester (= tricaine methane sulfonate, = MS 222) at an initial concentration of 75 mg per liter of distilled water, followed by an additional 100 mg per liter of water every 6 hr, (2) unbuffered sodium pentobarbital (= nembutal) at an initial concentration of 100 mg per liter of distilled water, followed by an additional 50 mg per liter of water every 6 hr, and (3) a single dose of 10 mg of chloral hydrate per liter of distilled water. Each anesthetic was used on an individual test group. Animals of both species were anesthetized with each treatment for 36 hr in distilled water. A second stage in the anesthetization process was the addition of 2-phenoxyethanol administered at about 2 mL per animal with a pipette close to the incurrent apertures; this treatment followed all primary anesthetics for a duration of 12 hr. Specimens from each anesthetization treatment were then separated into two groups per species and per treatment. One group of specimens from each species and anesthetic treatment was placed directly into 70% ethanol without fixation, while the other group of specimens from each species and anesthetic treatment was taken from anesthetic

Table 1

Comparison of results of various preservation methodologies in two species of *Elliptio* (Bivalvia: Unionidae).

Treatment†	Branchial (incurrent) papillae of			
	LACM	<i>E. i. occulta</i>	LACM	<i>E. d. monroensis</i>
Killed in A	92-49.3*	severe contraction		not tested
Killed in G	92-49.4*	severe contraction		not tested
N→A	92-49.9	severe contraction	92-50.6*	severe contraction
C→A	92-49.8	moderate contraction		not tested
T→A		not tested	92-50.5	moderate contraction
N→A→G→A	92-49.9b	moderate contraction		not tested
C→A→G→A	92-49.8b*	moderate contraction		not tested
T→A→G→A		not tested		not tested
N→G→A	92-49.5	severe contraction	92-50.3*	severe contraction
C→G→A	92-49.7*	extended		not tested
T→G→A	92-49.6*	fully extended	92-50.4*	fully extended

† Key to abbreviations of treatments: A = 70% ethyl alcohol; C = chloral hydrate; G = 20% glutaraldehyde; N = sodium pentobarbital (nembutal); T = 3-aminobenzoic acid ethyl ester (tricaine methane sulfonate).

* Illustrated herein.

and fixed in buffered 20% glutaraldehyde for 12 hr, rinsed in running tap water for 30 min, and then placed into 70% ethanol.

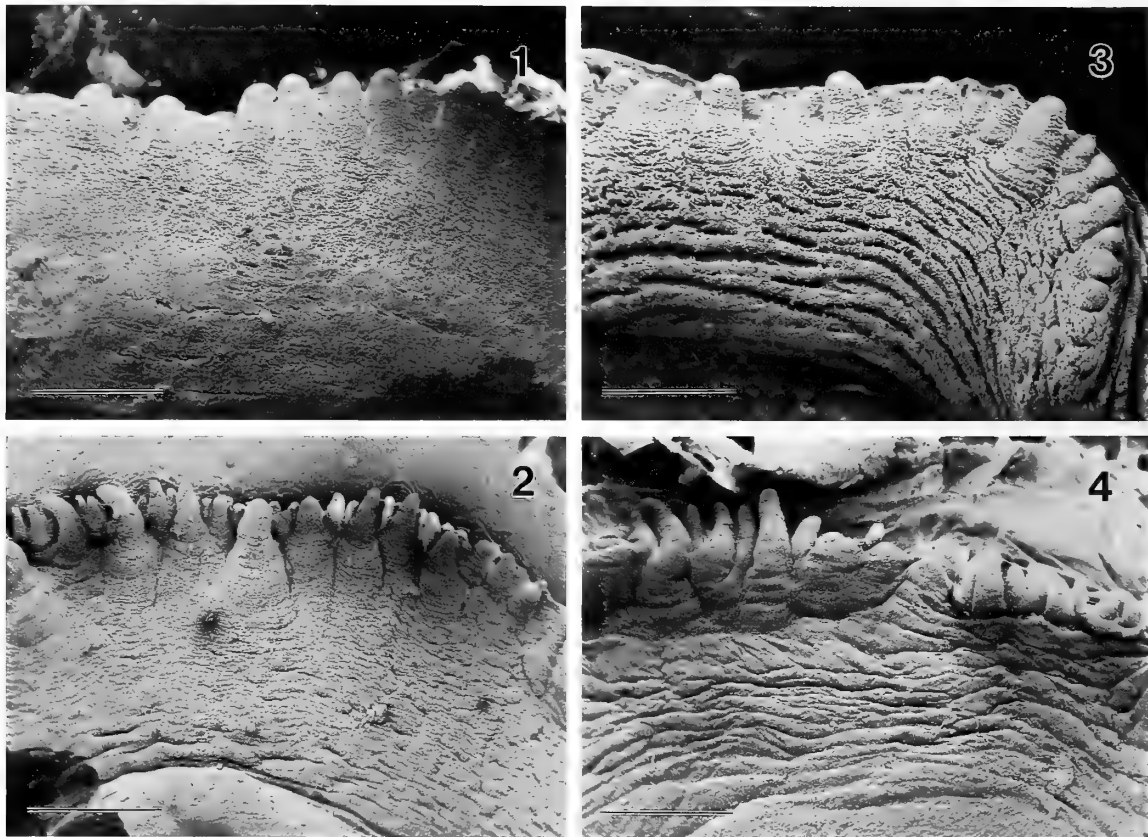
Because of the extensibility of the branchial, or incurrent, papillae in life, as well as their taxonomic value, I selected these tissues for study to determine the best anesthetization and fixation methodology. Additionally, ctenidial ciliary structures of *Lampsilis* sp. (LACM 92-71.3) were investigated for the effects of anesthetization upon these structures. With the exceptions of LACM 92-49.8 and LACM 92-49.9, which were adult males, all individuals selected for examination were adult females. For each specimen, the entire posterior mantle margin, inclusive of all branchial, or incurrent, papillae or ctenidia, was excised using small scissors under a dissecting microscope. These tissues were then placed into individual vials containing 70% ethanol and labeled by species and treatment. Critical point drying of the tissues was accomplished by upgrading alcohol content from 70% to 95% to 100% ethanol, then transferring tissues to a mixture of 50% absolute ethanol and 50% hexamethyldisilizane, and finally to 100% hexamethyldisilizane. Labeled tissues were placed in clean watch glasses and allowed to dry at room temperature under a chemical fume hood. Dried tissues were mounted on Cambridge S-4 SEM stubs, gold coated, and examined with a Cambridge 360 scanning electron microscope. All micrographs were taken at a consistent magnification of 25×

RESULTS

The results of the various experimental methodologies employed in this study on the contraction or extension of the branchial, or incurrent, papillae are summarized in Table 1.

As expected, the branchial papillae of two specimens of *Elliptio icterina* s.l. [= "*Unio*" *occulta*] that were pegged

open and placed alive in 70% ethanol exhibited severe contraction (Figure 1). Severe contraction of the branchial papillae also occurred in two specimens of this same taxon that were pegged open and placed alive in 20% glutaraldehyde (Figure 2). In both *Elliptio icterina* s.l. [= "*Unio*" *occulta*] and *Elliptio dariensis* s.l. [= "*Unio*" *monroensis*], moderate to severe contraction of the branchial papillae occurred when fully anesthetized specimens were placed in 70% ethanol without the benefit of fixation with glutaraldehyde (Figure 3). Specimens of either species that had been previously anesthetized and preserved in 70% ethanol, and then fixed in glutaraldehyde, exhibited moderate, but not severe, contraction (Figure 4). Those treatments that involved an initial anesthetic, and a secondary introduction of 2-phenoxyethanol, followed by glutaraldehyde fixation of fully anesthetized specimens, produced remarkably different results. The employment of unbuffered nembutal alone as the initial anesthetic resulted in severe contraction of the branchial papillae in both species tested (Figure 5); however, the foot of these animals expanded moderately, a response that would generally indicate that anesthetization was successful. On the other hand, the foot of those specimens treated with chloral hydrate remained contracted and the valves of the shell simply gaped open upon anesthetization. However, the branchial papillae of two specimens so tested exhibited extension (Figure 6), thus indicating that anesthetization did occur. The methodology that produced the best and most consistent results was treatment with 3-aminobenzoic acid ethyl ester for 24 hr, followed by 2-phenoxyethanol for 12 hr, with fixation in 20% glutaraldehyde for 12 hr, followed by a 30 min continuous rinse in tap water, with final preservation in 70% ethanol. Both the foot and the branchial papillae of both species tested exhibited full and complete extension when subjected to 3-aminobenzoic acid ethyl ester as the initial anesthetic (Figures 7, 8). The laterofrontal cilia of the ascending lamella of the outer



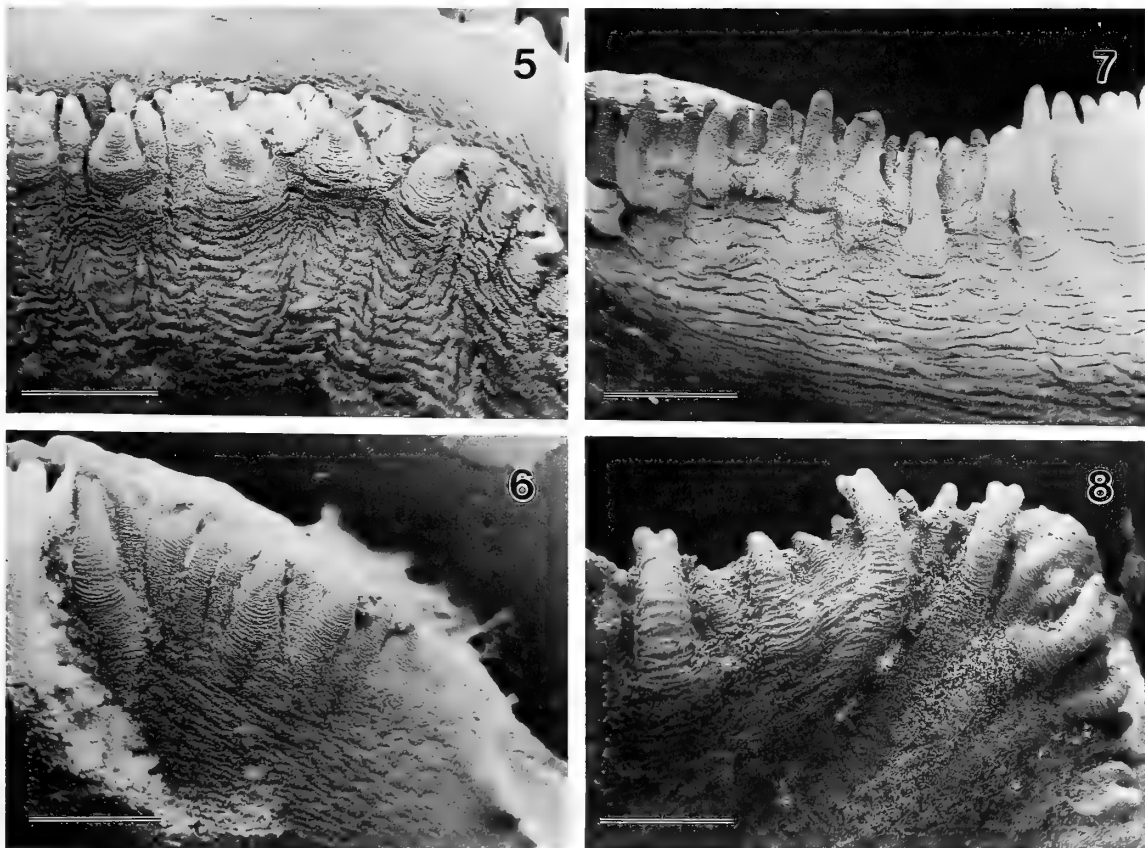
Explanation of Figures 1 to 4

Figures 1–4. Comparison of branchial papillae resulting from various experimental preservation methodologies that have not benefited by fixation between relaxation and preservation in 70% ethanol. Figure 1. *Elliptio icterina* s.l. [= "*Unio*" *occulta*], LACM 92-49.3, showing severe contraction of papillae resulting from being pegged open and placed living into 70% ethanol. Scale bar = 1 mm. Figure 2. *Elliptio icterina* s.l. [= "*Unio*" *occulta*], LACM 92-49.4, showing severe contraction of papillae resulting from being pegged open and placed living into 20% glutaraldehyde. Scale bar = 1 mm. Figure 3. *Elliptio dariensis* s.l. [= "*Unio*" *monroensis*], LACM 92-50.6, showing severe contraction following relaxation with nembutal and then preservation in 70% ethanol without the benefit of fixation in 20% glutaraldehyde. Scale bar = 1 mm. Figure 4. *Elliptio icterina* s.l. [= "*Unio*" *occulta*], LACM 92-49.9b, showing moderate contraction of papillae that have been relaxed with nembutal, preserved in 70% ethanol, then fixed in glutaraldehyde and preserved again in 70% ethanol. Scale bar = 1 mm.

demibranch of the ctenidia of *Lampsilis* sp. (LACM 92-71.3) that had undergone ideal anesthetization and fixation were found to be deployed in a lifelike configuration resembling a net, apparently so extended for the purpose of filtration (Figures 9–11).

In recent experimentation, I have found that when 100 mg of nembutal per liter of distilled water, buffered to a pH of 7.5 with Trizma HCl for tissue culture, is used as the initial anesthetic for 6 hr, followed by 3-aminobenzoic acid ethyl ester for 12 hr, and then by 2-phenoxyethanol for 12 hr, the amount of time needed to achieve full anesthetization of specimens is reduced significantly, and full extension of foot and branchial papillae is obtained. Further experimentation with this three-stage process with nembutal as the primary anesthetic has resulted in suc-

cessful anesthetization of both freshwater genera (e.g., *Amblesma*, *Quadrula*, and *Unio*) and marine venerid genera (e.g., *Mercenaria*), all of which have been difficult to anesthetize satisfactorily. Additionally, for chemically sensitive unionaceans such as the lampsilines, excellent, lifelike relaxation of tissues may be achieved by omitting the use of 3-aminobenzoic acid ethyl ester as an intermediate anesthetic and following through with continued additions of buffered nembutal at 100 mg per liter every 6 hr until the foot exhibits a significant decrease in tactile responsiveness, at which time a few drops of 2-phenoxyethanol should be administered by pipette on the floor of the container near the incurrent aperture. Fixation with buffered 20% glutaraldehyde buffered with collidine or sodium di-phosphate, following successful anesthetization by the above



Explanation of Figures 5 to 8

Figures 5-8. Comparison of branchial papillae resulting from various experimental preservation methodologies that utilize fixation in glutaraldehyde between various relaxation techniques and final preservation in 70% ethanol. Figure 5. *Elliptio dariensis* s.l. [= "*Unio*" *monroensis*], LACM 92-50.3, showing severe contraction of papillae resulting from relaxation with nembutal, followed by 2-phenoxyethanol, fixation in 20% glutaraldehyde, and preservation in 70% ethanol. Scale bar = 1 mm. Figure 6. *Elliptio iceterina* s.l. [= "*Unio*" *occulta*], LACM 92-49.7, showing partial extension of papillae resulting from relaxation with chloral hydrate, followed by 2-phenoxyethanol, fixation in 20% glutaraldehyde, and preservation in 70% ethanol. Scale bar = 1 mm. Figure 7. *Elliptio iceterina* s.l. [= "*Unio*" *occulta*], LACM 92-49.6, showing full extension of branchial papillae resulting from relaxation with 3-aminobenzoic acid ethyl ester, followed by 2-phenoxyethanol, fixation in 20% glutaraldehyde, and preservation in 70% ethanol. Scale bar = 1 mm. Figure 8. *Elliptio dariensis* s.l. [= "*Unio*" *monroensis*], LACM 92-50.4, showing full extension of branchial papillae resulting from relaxation with 3-aminobenzoic acid ethyl ester, followed by 2-phenoxyethanol, fixation in 20% glutaraldehyde, and preservation in 70% ethanol. Scale bar = 1 mm.

methodology, is mandatory for accurate lifelike anatomical preservation.

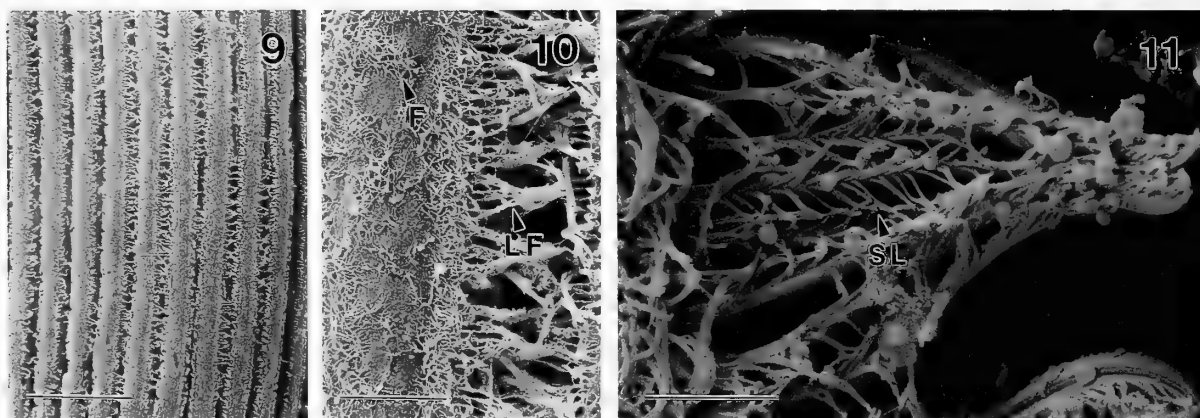
DISCUSSION

A review of the Materials and Methods sections of a surprisingly large number of papers reporting anatomical results for the purpose of justification of new species descriptions, or taxonomic revisions, within a wide diversity of mollusks (*e.g.*, Unionidae, Pisiidae, Hydroiidae, *etc.*) revealed a failure to document any methodology employed in the anesthetization or fixation of molluscan tissues. A few of the more recent papers dealing with the comparative

anatomy of members of the Unionoida that give no indication of the anesthetization and fixation methodology used include McMICHAEL & HISCOCK (1958), PAIN & WOODWARD (1964), and SMITH (1979).

A variety of anesthetization and fixation methodologies have been proposed for use on diverse molluscan taxa. FLORKIN (1941) is the only author to specifically address the problem of anesthetization of unionid bivalves. He evaluated the effects of four different barbiturates on *Anodonta* and found nembutal to be the most effective of those tested.

MORCH (1868) was apparently the first to recommend the addition of a chemical anesthetic (*i.e.*, tobacco) in the



Explanation of Figures 9 to 11

Figures 9–11. Ciliation of the ascending lamella of the outer demibranch of the ctenidia of *Lamprosis* sp. (LACM 92-71.3) following anesthetization and fixation via the primary recommended methodology (see Text). Figure 9. General overview of the surface of the ascending lamella showing the arrangement of filaments and the location of Figure 10 as shown by rectangle outline. Scale bar = 200 μ m. Figure 10. Magnified portion from central area of Figure 9 showing a single ctenidial filament with reduced frontal cilia (F) and fully extended laterofrontal cilia (LF) in apparent natural position for filtering. Scale bar = 25 μ m. Figure 11. Highly magnified network of a single cluster of laterofrontal cilia showing the secondary microlaterofrontal cilia (SL) fully extended between the primary laterofrontal cilia fronds. Also seen are calcium phosphate concretions known to occur in the demibranchs of Unionaceans (see MCMAHON, 1991). Scale bar = 5 μ m.

preparation of mollusks for anatomical study, in this case pulmonate gastropods. A general review of methodologies is given below by technique.

Techniques

Freezing: GOHAR (1937) has recommended slowly freezing nudibranch gastropods, Paul Scott (personal communication, 1992) has successfully used freezing to relax a variety of marine gastropods, and A. H. Clarke (personal communication, 1991) observed that he had successfully relaxed freshwater unionids by slowly freezing them.

Recently, I received an overnight shipment of live unionids in which too much synthetic ice was used in layers above and below the plastic bags containing the bivalves. Upon opening the box, I found that all specimens were frozen. Although this was not a controlled experiment, it provided an unexpected opportunity to evaluate freezing as a method for relaxation of unionid bivalves. The results, however, were mixed, as different genera reacted in completely different ways to freezing. Poor results were exhibited by various species of *Elliptio*, as the posterior mantle margins had pulled away from the shell, curled inward, and contracted in death. Quite the opposite effect was observed in *Villosa*, as freezing produced some beautifully relaxed material in this genus.

Cocaine: DALL (1892) recommended a 1% solution of cocaine, a legal substance at the turn of the twentieth century, for the anesthetization of mollusks in general. SIEBERT (1913) successfully used a 1% solution of cocaine to anesthetize *Anodonta cellensis* followed by fixation with

Zenker's solution and Flemming's solution. However, SCHWANECKE (1913) reported that cocaine was unreliable for successful anesthetization of *A. cellensis*, and that an overnight exposure to a 3–4% solution of ammonium chloride, followed by fixation with glacial acetic acid, produced the desired results in his study of the circulatory system of this species. As cocaine is a controlled substance, and therefore not readily available to most students of bivalve comparative anatomy, its usefulness as a bivalve anesthetic was not investigated here.

Menthol: I have successfully employed menthol to anesthetize aquatic pulmonate gastropods, and Paul Scott (personal communication, 1992) has had successful results in using menthol to anesthetize marine bivalves of the family Cardiidae, but I have not found menthol to be effective in the anesthetization of unionids. ABDEL-MALEK (1951) reported menthol to be useful in the anesthetization of helminths, and menthol serves as one of the ingredients in more complex anesthetization formulas of McCRAW (1958) and of VAN EEDEN (1958); however, VAN DER SHALIE (1953) noted that menthol produced unpredictable results in pulmonates. GOHAR (1937) reported that tissue maceration occasionally occurred prior to anesthetization using menthol, and RUNHAM *et al.* (1965) reported that menthol used alone took a prolonged time to take effect, which may explain the maceration reported by GOHAR (1937). Successful anesthetization of hydrobiid gastropods using menthol, followed by tissue fixation using either formalin or Bouin's solution, was accomplished by THOMPSON (1968, 1984) and by HERSHLER & THOMPSON (1992).

Magnesium chloride: LEIBOWITZ (1976) recommended the use of magnesium chloride as an initial anesthetic for marine gastropod veliger larvae, followed by propylene phenoxetol as a second stage anesthetic. STIRLING *et al.* (1984) used magnesium chloride as a primary stage anesthetic, followed by benzocaine (ethyl-4-aminobenzoate) and procaine hydrochloride to anesthetize the veliger larvae of the marine pulmonate *Amphibola crenata*. RUNHAM *et al.* (1965) reported excellent anesthetization results for pulmonates by injecting them with a 10% solution of magnesium chloride. CHUNG (1985) reported that a solution consisting of 2% magnesium chloride and 0.01% succinylcholine chloride produced ideal results when injected into *Helix aspersa* Muller. AVELAR & SANTOS (1991) used magnesium chloride to relax *Castalia undosa undosa* of the freshwater bivalve family Hyriidae; however, I do not recommend magnesium chloride for unionids as I have observed unionids to react negatively—the introduction of a 1% solution caused contraction and death.

Succinylcholine chloride: BEEMAN (1968) and MATERA & DAVIS (1982) used an injection of succinylcholine chloride in a seawater solution to anesthetize nudibranch gastropods. BURTON (1975) anesthetized *Helix pomatia* by injecting individuals with succinylcholine chloride, and CHUNG (1985) used this in combination with magnesium chloride to anesthetize *Helix aspersa*. But I have not explored the use of succinylcholine chloride as an anesthetic for freshwater bivalves.

Chloral hydrate: Chloral hydrate was recommended for the anesthetization of opisthobranch gastropods by ARIAS *et al.* (1985). VAN EEDEN (1958) used a combination of menthol and chloral hydrate followed by immersion of extended pulmonates in boiling formalin; however, EMBERTON (1989) reported that chloral hydrate was only partially successful as an anesthetic for pulmonates. The present study demonstrates that chloral hydrate is not an ideal anesthetic for unionid bivalves.

2-phenoxyethanol: Propylene phenoxetol was used by OWEN (1955) to anesthetize marine bivalves; it also was used for marine and terrestrial gastropods (OWEN & STEEDMAN, 1958) with variable results. RUNHAM *et al.* (1965) used propylene phenoxetol in combination with nembital to successfully anesthetize pulmonate slugs. Propylene phenoxetol is no longer available from chemical supply houses in the United States; however, a related compound, 2-phenoxyethanol, is a satisfactory substitute, and its effect on the anesthetization of unionid bivalves is discussed in this study.

3-aminobenzoic acid ethyl ester: This chemical, also known as tricaine methane sulfonate, methanesulfonate salt, and M.S. 222, was first reported to be highly successful in the anesthetization of cold blooded animals, in this case frogs, by ROTHLIN (1932). The chemical 3-aminobenzoic acid ethyl ester has been used as a component of a variety of chemical treatments in the course

of anesthetization of various aquatic pulmonates by JOOSSE & LEVER (1959), LEVER *et al.* (1964), LIEBSCH *et al.* (1978), and MUTANI (1982). Attempts by Roland Anderson, Seattle Aquarium (personal communication) to anesthetize *Anodonta oregonensis* and *A. kennerlyi* using Finquel MS 222 have failed to produce satisfactory results, and I suspect that this failure is due to an industrial defect in chemical purity, rather than other factors, as I have achieved excellent results using 3-aminobenzoic acid ethyl ester on *A. kennerlyi* that were collected from the same locality and habitat as were those that Roland Anderson attempted to anesthetize. The results of anesthetization of unionids using 3-aminobenzoic acid ethyl ester are documented in this study.

Nembital: I have found nembital (= sodium pentobarbital) to produce excellent results in pulmonates, and, if correctly buffered, to be an important primary stage anesthetic for freshwater unionids such as *Amblema*, *Quadrala*, and *Uniomorus*, as well as marine venerid bivalves such as *Mercenaria*, all of which I have found to be difficult to anesthetize satisfactorily. VAN DER SHALIE (1953) recommended a 10% solution of nembital for the anesthetization of the terrestrial prosobranch gastropod *Pomatiopsis*. MEIER-BROOK (1976) reported excellent results for freshwater pulmonates, prosobranchs, and *Pisidium* spp. using pentobarbital acid, advising that this is superior to nembital; however, HEARD (1965) employed a 10% solution of nembital to successfully anesthetize a variety of *Pisidium* species. Nembital has been reported to successfully anesthetize a variety of Unionidae, including *Fusconaia masoni* (Conrad, 1834) as studied by FULLER (1973), as well as several species in the genus *Lampsilis* (KRAEMER, 1981; KAT, 1983). BARKER (1981) presented observations supporting the use of nembital for the anesthetization of pulmonates. ZAWIEJA (1980) recommended the use of "Vet-butal," or veterinary nembital, for the anesthetization of *Lymnaea stagnalis* (Lymnaeidae). JOURDANE & THERON (1980) successfully anesthetized *Biomphalaria glabrata* (Planorbidae) using a 0.08% solution of nembital. RUNHAM *et al.* (1965) reported excellent results from using a 0.08% solution of nembital, followed by a 1% solution of propylene phenoxetol, to anesthetize pulmonate slugs. Nembital has been used with other chemicals for the anesthetization of mollusks in a variety of combinations. MCCRAW (1958) used nembital followed by the addition of menthol to anesthetize aquatic pulmonate gastropods, and KEAWJAM (1986) reported that menthol followed by nembital was useful in the anesthetization of *Pila* (Pilidae). JOOSSE & LEVER (1959) used nembital followed by M.S. 222 (= tricaine methane sulfonate, = 3-aminobenzoic acid ethyl ester) to anesthetize *Lymnaea*; and LEVER *et al.* (1964) has combined nembital and M.S. 222 with water that has been aerated with N₂ and CO₂ gases for the anesthetization of aquatic pulmonate gastropods. LIEBSCH *et al.* (1978) modified the method of LEVER *et al.* (1964) by using a 0.1% solution of nembital aerated first with CO₂ gas,

followed by aeration with N₂ gas to anesthetize specimens of *Biomphalaria glabrata*. MUTANI (1982) successfully used the method described by JOOSSE & LEVER (1959) to anesthetize aquatic pulmonates; however, KEAWJAM (1986) found the method of JOOSSE & LEVER (1959) to be unsatisfactory on specimens in the Pilidae. The effects of nembutal on unionids is discussed in this study.

Other methodologies: A few other unusual methodologies have been employed in the anesthetization of mollusks and are mentioned briefly here. CARRIKER & BLAKE (1959) utilized Sevin (1-naphthyl N-methyl-carbamate) followed by killing on dry ice to successfully anesthetize muricid gastropods, and HOFFMAN (1986) recommended the addition of acetone to Sevin, a rather insoluble compound, to act as an aid in dissolving this compound into seawater. BAILEY (1969) used carbon dioxide from dissolving dry ice in water to anesthetize slugs. GREGG (1944) recommended simply drowning land slugs to relax them, and HUBRICHT (1951) recommended the addition of a saturated solution of Chloretone to the drowning process for land slugs. Chloretone was also used by CLEMENT & CATHER (1957) in the anesthetization of marine gastropod veliger larvae. PRINCE & FORD (1985) experimented with both diethyl carbonate and ethanol in the anesthetization of the marine abalone *Haliotis ruber* and found ethanol to be both safer and more effective than diethyl carbonate. DE WINTER (1985) used a 10% to 25% solution of ethanol to anesthetize and kill slugs. Amylocaine hydrochloride at 1% (= Stovaine) has been used by SMITH (1961) on nudibranchs. Althesin, benzyl alcohol, ethanol, nembutal, and xylazine were all used experimentally by BOURNE (1984) to anesthetize the moon snail *Polinices lewisii*, with xylazine demonstrating the best results. Urethane (= ethyl carbamate) has been used for anesthetization of aquatic pulmonate gastropods by MICHELSON (1958), ether for anesthetization of terrestrial pulmonate gastropods by RIPPLINGER & JOLY (1960), and thin leaves of celluloid in photoxilin ether for anesthetization of *Anodonta* by KOCH (1916). Successful anesthetization of *Lymnaea stagnalis* (Lymnaeidae) using halothane, enflurane, and isoflurane was reported by GIRDLESTONE *et al.* (1989).

RECOMMENDATIONS FOR FRESHWATER BIVALVES

Complete immobility of the holding pans is necessary for the anesthetization treatments to be successful. This is best done in a controlled laboratory environment, rather than in the field. When in the field for extended periods of time, I have kept freshwater bivalves alive for a week while traveling in a hot car in the deep south of the United States by keeping the animals on ice in sturdy ice chests with a change of ice every 24 hr. Freshwater bivalves should be anesthetized with one of the following methodologies: (1) add 75 mg of 3-aminobenzoic acid ethyl ester per liter of distilled water initially, followed by an additional 100 mg of 3-aminobenzoic acid ethyl ester at 60 hr

intervals for 24 to 120 hr, or until the foot exhibits little response to stimuli, followed by a few drops of 2-phenoxyethanol introduced via pipette on the base of the container near the incurrent aperture for 12 to 24 hr, or (2) 100 mg of nembutal per liter of distilled water buffered to a pH of 7.5 with Trizma HCl for tissue cultures for the first 24 hr, followed by 100 mg per liter of 3-aminobenzoic acid ethyl ester, followed by a few drops of 2-phenoxyethanol for 12 to 24 hr (a recommended procedure for tenacious, thick-shelled bivalves such as *Quadrula*), or (3) 100 mg of nembutal per liter of distilled water buffered to a pH of 7.5 with Trizma HCl for tissue culture for 48 to 72 hr, omitting the use of 3-aminobenzoic acid ethyl ester, followed by a few drops of 2-phenoxyethanol as response to stimuli fails (a recommended procedure for the more delicate lampsilines).

After the species have acclimated to a holding pan of native or distilled water and have begun siphoning and moving about, 75 mg of 3-aminobenzoic acid ethyl ester per liter of distilled water should be lightly sprinkled over the surface of the water initially, followed by 100 mg of 3-aminobenzoic acid ethyl ester per liter every 6 hr. One may determine when it is time to add the 2-phenoxyethanol by probing the extended foot. If a significantly reduced reaction to this stimulus is observed, then the specimen is ready for the addition of 2-phenoxyethanol. Using an eyedropper, 2-phenoxyethanol should be introduced on the bottom of the holding pan close to the posterior siphons and the specimen should be allowed to continue anesthetization for another 12 hr. Some experimentation with quantities of anesthetics and time of treatment may be required to determine what combination works best for each genus. Care should be taken to separate genera into separate pans for anesthetization, as species in many genera anesthetize at very different rates. For example, *Lampsilis*, *Villosa*, and other Lampsilini tend to anesthetize rather quickly (24 hr); *Elliptio*, *Pleurobema*, and other Pleurobemini take longer to show results; and such Amblemini as *Quadrula* and *Megaloniais* may take up to 120 hr to anesthetize, if buffered nembutal is not employed as the initial anesthetic. If genera are mixed in the holding pans, those that anesthetize earliest may begin to macerate and foul the water, causing those that would tend to anesthetize later to retract and not anesthetize properly.

pH: Proper control of pH is fundamental to both the anesthetization and the fixation of mollusks, and this is especially true for freshwater bivalves. TOWNSEND (1973) found that nembutal buffered with acetate to a slightly acidic pH (6.0) was helpful in the anesthetization of the planorbid snail *Biomphalaria glabrata*. Improved techniques for the successful anesthetization of *Helisoma duryi* (Planorbidae) by KUNIGELIS & SALEUDDIN (1984) using nembutal was enhanced by regulating increase in pH, caused by the ionization of nembutal, with Trizma buffer. In these two studies, buffers were used to extend the life of near neutral pH during anesthetization with barbitu-

rates of a high pH, thus enhancing tissue penetration by the un-ionized anesthetic. Barbiturates have a high pH, and are used occasionally by chemists as buffering agents. Aldehydes, on the other hand, tend to have an acidic pH (3–6), and HOLT & HICKS (1961) have reported that barbiturate buffers tend to react adversely with aldehydes. J. D. Williams (personal communication) found that freshwater bivalves tend to contract into their shells when placed in an aldehyde fixative following complete anesthetization of the animals using unbuffered nembutal. KITIKOON & RIVERA (1982) found it highly useful to kill specimens of *Tricula* (Hydrobiidae) with Curarine following anesthetization with nembutal to keep the animals from retracting into their shells in response to glutaraldehyde fixation; however, they did not explore the reason behind this contraction response. In this study, animals anesthetized with unbuffered nembutal and fixed with glutaraldehyde exhibited pronounced contraction of the branchial papillae (see Figures 3, 5). I suspect that this contraction is a physiological response to a marked difference in the pH of the anesthetic and that of the fixative. Maintenance of near neutral pH during nembutal anesthetization will not only enhance the penetration effect of the nembutal into the tissues, but may also be useful in controlling stimulus/response reactions of anesthetized animals to pH changes resulting from the fixative, even though the fixative has been buffered to a neutral pH, because as the aldehyde polymerizes in the presence of a buffer (HAYAT, 1981), pH undoubtedly fluctuates.

Fixatives: ELLIS (1978) recommends the use of 70% industrial alcohol to preserve unionid specimens, and WOODWARD (1964, 1965, 1969) cites "spirit" (presumably ethyl alcohol) preserved specimens in his studies. Some authors (VEITENHEIMER & MANSUR, 1978; FULLER, 1972) have stated that tissue fixation has been accomplished using 70% alcohol, or ethanol. Students of molluscan comparative anatomy should be wary of studies that state that tissue fixation was achieved using any type of alcohol. Alcohol is definitely not a tissue fixative; rather it dehydrates cells and tissues, thus causing pronounced tissue shrinkage and consequent morphological distortion. "The main objectives of fixation are to preserve the structure of cells with minimum alteration from the living state with regard to volume, morphology, and spatial relationships of organelles and macromolecules, minimum loss of tissue constituents, and protection of specimens against subsequent treatments including dehydration, embedding, staining, vacuum, and exposure to the electron beam" (HAYAT, 1981).

Aldehydes such as formaldehyde, acrolein, glutaraldehyde, as well as other chemicals, particularly osmium tetroxide, have been used to fix tissues. For mollusks, the choice of an appropriate fixative is of critical importance. SOLEM *et al.* (1981) reported that land molluscan material that had been fixed in buffered formalin and subsequently transferred to alcohol became unusable in 2 to 4 years. Several studies have been based on unanesthetized speci-

mens that had been initially fixed in 8–10% formalin and transferred to 70% ethanol, a practice recommended by MURRAY & LEONARD (1962) and McMAHON (1991), and employed by CASTAGNOLO *et al.* (1980), and MANSUR & SILVA (1990), or preservation in a mixture of formalin & alcohol (KILIAS, 1956). On the other hand, HAYAT (1981) noted that "no other fixative has surpassed glutaraldehyde in its ability to cross-link and preserve tissue proteins for routine electron microscopy." I have used buffered glutaraldehyde to fix anesthetized unionids with excellent results, and tissues so fixed have remained in good condition for the past three years. A few studies of gill ciliation apparently have not found it necessary to employ anesthesia in order to obtain results. WAY *et al.* (1989) injected living unionids with a 2% solution of glutaraldehyde in 0.1 M Sorenson's phosphate buffer, and TANKERSLEY & DIMOCK (1992) dissected living unionids and placed the ctenidia in a 2% solution of glutaraldehyde in 0.2 M Sorenson's phosphate buffer and post-fixed the tissues in a 2% solution of cacodylate buffered osmium tetroxide. I have found that the laterofrontal cilia of the ascending lamella of the outer demibranch of the ctenidia of *Lampsilis* sp. (LACM 92-71.3) that have undergone ideal anesthetization and fixation are deployed in a lifelike configuration resembling a net, apparently so extended for the purpose of filtration (Figures 9–11). This observation of what is apparently the natural position of the laterofrontal cilia of the ctenidia differs significantly from the position of these cilia as described by workers who simultaneously killed the animals and fixed the tissues in buffered 2% glutaraldehyde without the benefit of anesthesia (WAY *et al.*, 1989).

HAYAT (1981) provided an excellent review of buffering chemicals for various fixative agents and their properties. Of those, I have found that sodium bicarbonate serves as a useful, inexpensive, and non-toxic buffer for tissue fixation using glutaraldehyde. Both TANKERSLEY & DIMOCK (1992) and WAY *et al.* (1989) successfully used sodium diphosphate to buffer glutaraldehyde to a pH of 7.2 for fixation of unionids. HAYAT (1981) gave high marks to collidine as a buffer for glutaraldehyde, and I have found collidine to be a more efficient buffer than sodium bicarbonate or sodium diphosphate. As any increase in pH above neutral accelerates polymerization and consequent deterioration of glutaraldehyde, a buffered stock solution has a limited shelf life. However, I have successfully reused a buffered 20% solution of glutaraldehyde several times over before the solution exhibited noticeable polymerization, as may be detected when the glutaraldehyde turns a dark yellow color. It is best to filter the fixative solution between uses to avoid contamination with glochidia from previous uses. Glutaraldehyde will deteriorate via polymerization with time, and this deterioration accelerates rapidly as a result of either a sharp rise in either temperature or pH. Deterioration of glutaraldehyde can be minimized by storing it as an unbuffered 25% solution at subfreezing temperatures (–20°C). Glutaraldehyde is

a hazardous chemical and the use of rubber gloves and a chemical fume hood is imperative. Use of chemical fume mask and protective eye goggles are strongly recommended. Following fixation, the specimens should be rinsed under gently flowing tap water for about 30 min and then preserved in 70% ethanol. If ethanol is not available, 50% isopropyl alcohol can be used as a temporary preservative. Permanent storage in isopropyl alcohol will harden the soft parts over time. Some workers prefer to add 1–3% glycerine to their alcohol-preserved specimens (McMAHON, 1991) so that the soft bodies will be kept moist should the alcohol evaporate over time; however, TURNER (1976) cautioned against the use of glycerol if specimens are to be examined using SEM analysis. I suspect that glycerol-treated specimens would result in undesirable coating of ciliary tracts or other fine surface structures of the anatomy, and also recommend against its use.

SUMMARY

Chemically induced anesthetization of freshwater mussels is of critical importance to the bivalve anatomist, as it allows the animal to be preserved in lifelike condition; however, unless such anesthetization is followed by tissue fixation in a suitable fixative, the results will be unsatisfactory.

The anesthetic 3-aminobenzoic acid ethyl ester, followed with 2-phenoxyethanol, and fixation with glutaraldehyde, has been demonstrated here to produce reliably anesthetized anatomical specimens. A. Lopez has used this method in his laboratory in Managua, Nicaragua, with outstanding success on both Nicaraguan Mycetopodidae (Etheriacea) and Unionidae. As noted above, much time may be saved, and some genera that are difficult to anesthetize may benefit substantially, by the use of buffered nembital as the initial anesthetic if it is then followed by the procedure recommended in this paper. Nembital is the anesthetic of choice for pulmonate gastropods, but produces unsatisfactory results when used alone and unbuffered on freshwater unionid bivalves. Use of chloral hydrate is not recommended. Although it produced moderate extension of the branchial papillae, the foot remained completely contracted and this condition would be counterproductive to any exploration of the coiling of the digestive tract within the foot.

Without proper fixation, however, anesthetization efforts will fail, because anesthetized, or even apparently dead, specimens will undergo tissue contraction when placed directly into 70% ethanol. Tissue contraction will become severe when unfixed tissues are taken through a graded alcohol series to absolute alcohol and then into hexamethyldisilazane to obtain critically dried tissues for SEM analysis. A freshly buffered 20% solution of glutaraldehyde is the preferred fixative, and 12 hr an ideal fixation time.

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NOTES, INFORMATION & NEWS

Effects of Restricted Food Intake on Hemolymph Glucose Concentration and Digestive Gland-Gonad Lipid Level in the Schistosome Vector *Biomphalaria glabrata* (Say) (Gastropoda: Planorbidae)

by

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Introduction

The effects of starvation on storage metabolite levels have been examined in several mollusks. HEEG (1977), for example, demonstrated that lipid and carbohydrate reserves were reduced in the digestive gland and gonad of starved *Bulinus africanus* (Krauss). Similar depletion of lipid and carbohydrate reserves was reported in starved *Biomphalaria glabrata* by DUNCAN *et al.* (1987) and CHRISTIE *et al.* (1974), respectively. Moreover, several studies indicate that starvation was partially responsible for depletion of metabolic reserves in schistosome-infected snails. Hemolymph glucose and glycogen reserves in the digestive gland were reduced in *Biomphalaria glabrata* infected with *Schistosoma mansoni* Sambon, and these effects were similar to those observed during starvation of normal uninfected snails (CHRISTIE *et al.*, 1974; STANISLAWSKI & BECKER, 1979). On the basis of these and other observations, BECKER (1980) concluded that the parasite exerts profound effects on host metabolism by competing with host tissues for nutrients, thus inducing a state of starvation. Such nutritional competition, however, would not result in starvation per se, but rather, would reduce the availability of assimilated nutrients for snail tissues. Previous investigation has demonstrated that food consumption and assimilation were unaffected by infection, but snail conversion efficiency was significantly reduced in infected individuals (THOMPSON & MEJIA-SCALES, 1989). Because maturation and cercarial shedding of *S. mansoni* occur in a continuous daily cycle (JOURDANE & THERON, 1987), nutritional stress caused by infection may follow a similar diurnal rhythm.

In contrast to the effects of schistosome infection on carbohydrate reserves, recent studies demonstrated that infection by *Schistosoma mansoni* caused an increased deposition of lipids in the digestive gland and gonad of *Biomphalaria glabrata*, supporting earlier histological observations by others on a variety of trematode-infected mollusks (PORTER, 1970). Previous studies with other metazoan invertebrates including some flatworms demonstrated decreased storage of carbohydrates, but accumulation of lipid during starvation (DAVIS & FRIED, 1977). CALLOW &

JENNINGS (1974) reported that lipid was utilized by triclad turbellarians during starvation, but lipid synthesis and deposition were increased in response to decreased or restricted food intake. Subsequently, CALLOW & JENNINGS (1977) suggested that many free-living metazoans that face unpredictable but likely periods of food shortage may have developed optimal metabolic strategies for accumulating sufficient storage reserves beforehand to survive during starvation. They demonstrated that maximum food storage in the flatworm *Dugesia lugubris* (Schmidt) did not correspond to maximum food availability, but to a submaximal level that signaled an impending period of food shortage. When animals were starved, their storage lipids decreased, but when pulse fed, that is, fed once/week, animals stored more lipid than individuals fed daily or every other day.

We hypothesize, based on the conclusion by BECKER (1980), that the increased lipid level in infected *Biomphalaria glabrata* may reflect a similar response to food shortage as that described above by CALLOW & JENNINGS (1977), in the case of *B. glabrata*, brought about by nutrient competition between the host and parasite. In the present study we attempted to mimic the effects of schistosome infection on hemolymph glucose and lipid levels in the digestive gland-gonad (DGG) by placing uninfected snails on a daily or weekly feeding regime. The effects of restricted food intake on storage metabolite levels in *B. glabrata* have not been previously examined.

Materials and Methods

Stock colonies of *Biomphalaria glabrata* (albino M line strain) were reared and maintained in the laboratory on fresh Romaine lettuce supplemented with Tetramin® fish food as described previously (THOMPSON, 1987). For feeding trials, three 2-gallon (7.5-L) bottomless aquaria each containing 45 snails were submerged in a single 15-gallon (57-L) aquarium. The smaller aquaria rested on a plastic grid (1 cm² sections) supported approximately 2 cm from the bottom of the larger aquarium. Fecal material accumulated under the grid and was inaccessible to the snails, which otherwise exhibit coprophagy. Snails were maintained in a commercial spring water (Arrowhead, Colton, California 92324) at room temperature, approximately 26°C, under a 16:8 hr light/dark photoperiod. The aquaria were cleaned and filled with fresh spring water each week.

Snails were treated in one of three ways: (1) fed whole lettuce *ad libitum*, (2) fed lettuce *ad libitum* once/week for 24 hr, or (3) fed daily with a reduced portion of lettuce comprised of a single 5-cm² section of leaf randomly torn into several smaller pieces, which were totally consumed within 2 to 4 hr. Experiments were conducted for four

Table 1

Effect of nutrient-deprivation on body and DGG (digestive gland-gonad complex) weight, lipid level, and hemolymph glucose concentration of *Biomphalaria glabrata*.

Nutritional treatment	% survival	Fresh weight (mg)		Mean lipid content ^b		Hemolymph glucose (mg%)
		Total body	DGG	μg/DGG	mg/g DGG	
Replicate 1 ^a						
<i>ad libitum</i>	96	307 ± 7*†	89 ± 3*†	1112	12.8	3.7 ± 0.2*
fed daily	80	150 ± 5*	42 ± 2*	431	10.4	4.6 ± 0.2*
fed 1/wk	60	135 ± 6†	40 ± 2†	368	9.0	6.3 ± 0.4*
Replicate 2 ^a						
<i>ad libitum</i>	70	179 ± 9*	55 ± 3*	645	11.8	3.4 ± 0.1
fed daily	50	138 ± 8*	41 ± 3*	380	9.3	3.2 ± 0.3
fed 1/wk	32	112 ± 6*	32 ± 2*	264	8.4	4.3 ± 0.6
Replicate 3 ^a						
<i>ad libitum</i>	70	202 ± 11*	64 ± 4*	732	11.2	4.6 ± 0.4
fed daily	40	166 ± 12*	47 ± 4*	508	10.7	5.1 ± 0.5
fed 1/wk	34	127 ± 8*	33 ± 3*	327	10.0	6.4 ± 0.9
Replicate 4 ^a						
<i>ad libitum</i>	80	ND	89 ± 5*†	1159	13.1	4.4 ± 0.4*
fed daily	62	ND	58 ± 3*	529	9.1	3.3 ± 0.8†
fed 1/wk	42	ND	47 ± 4†	428	9.2	8.1 ± 0.7*†

^a $\bar{x} \pm SE$, $n = \leq 43$ based on survival; numbers in columns followed by the same symbol are significantly different statistically at the 5% level as determined by Duncan's multiple range test.

^b Based on pooled sample.

ND = not determined.

weeks, a time period consistent with the beginning of patency in snails infected with *Schistosoma mansoni*. The hemolymph from individual snails was collected in capillary tubes by puncturing the heart through the shell. Snails were then gently crushed between two petri plates, the shell fragments carefully removed, and total body wet weight determined. The DGG was then dissected and weighed.

The total lipid of the DGG from each group was extracted from the pooled tissue in chloroform-methanol (1:2 v/v) by the method of BLIGH & DYER (1959). The quantity of the final washed lipid was determined gravimetrically. Hemolymph was deproteinized with $ZnSO_4 \cdot Ba(OH)_2$ and the glucose concentration determined by the oxidase-peroxidase method using a Sigma Diagnostics kit (Sigma Chemical Co., St. Louis, Missouri 63178). Standard glucose curves prepared with water or hemolymph gave the same results.

Statistical analysis of data was performed by ANOVA followed by comparison of means using Duncan's multiple range test.

Results

The results of feeding experiments with *Biomphalaria glabrata* were highly variable. Data, therefore, are presented in replicate form (Table 1). In all cases, body and DGG fresh weight were reduced in nutrient-deprived snails. The proportion of body weight represented by the DGG, however, was constant in all groups at $29.1 \pm 1.7\%$ for all

treatments in replicates 1 through 3. Snail mortality consistently increased with severity of food restriction.

The mean lipid content per individual DGG, as well as in relation to the weight of DGG, was lower in the nutrient-deprived snails compared with controls fed *ad libitum* (Table 1). Snails fed once/week had lower lipid levels than those that underwent daily but restricted feeding.

The hemolymph glucose of snails generally was elevated by nutrient deprivation and the results were diametrically opposite to those on lipid concentration (Table 1). That is, nutrient-deprived snails fed once/week had higher hemolymph glucose than those fed reduced rations daily. In most cases, however, glucose concentrations in the latter were not significantly different from those of snails fed *ad libitum*.

Discussion

During the present study, hemolymph glucose in *Biomphalaria glabrata* was maintained or increased by restricted food intake (Table 1). THOMPSON & LEE (1986) failed to observe any difference in hemolymph glucose between starved *B. glabrata* and snails fed *ad libitum*, although other studies demonstrated decreased hemolymph glucose in starved snails (STANISLAWSKY & BECKER, 1979). Our results with *B. glabrata* were similar to those of VELDHIJZEN (1975) with *Lymnaea stagnalis* (Linnaeus). Starvation failed to cause a depletion of hemolymph glucose in that species.

Moreover, a sharp rise in hemolymph glucose, similar to that observed during the present result with *B. glabrata* fed once/week, occurred in *L. stagnalis* when snails were fed following two weeks starvation. Hemolymph glucose was likely maintained at the expense of storage glycogen (CHRISTIE *et al.*, 1974), or trehalose (ANDERTON *et al.*, 1993) and hemolymph glucose level may provide a valuable indicator of this mobilization process in food-deprived snails.

The present results on hemolymph glucose levels in *Biomphalaria glabrata* whose food intake was restricted are in marked contrast to results of studies with infected snails. Investigations to date have consistently demonstrated decreased glucose levels in schistosome infected snails. This difference between infected and nutrient-deprived individuals may reflect differences in metabolic rates. Others have reported that respiration (*i.e.*, oxygen consumption) in *B. glabrata* was unaffected or was increased during infection, and the increase in oxygen consumption was the result of respiration of snail tissues and not due to parasite metabolism (LEE & CHENG, 1971; BECKER, 1980). In contrast, investigations with starved snails indicate that starvation causes a decrease in metabolic rate (WILLIAMS & GILBERTSON, 1983). Thus, mobilization of carbohydrate reserves may occur similarly during infection and food deprivation, but glucose level in snails deprived of food may be unaffected or increased because the snail's metabolic rate is reduced.

Storage lipids in *Biomphalaria glabrata* were depleted in a similar manner by restricted food intake as reported by DUNCAN *et al.* (1987) in starved snails. It appears, therefore, that the increased lipid previously observed in schistosome-infected individuals did not result from a parasite-induced food deprivation, in the manner hypothesized above. The role of lipid as a storage reserve in *B. glabrata* as well as other pulmonate gastropods is not clear. Although triglyceride may decrease during starvation in some species, glycogen appears to be the main storage metabolite utilized (CHRISTIE *et al.*, 1974; HEEG, 1977; VELDHUIJZEN, 1975). MEYER *et al.* (1986) failed to observe increased ketone body formation in starved *B. glabrata*, further indicating that lipid may not be an important energy reserve. Thus, the role of lipids in the metabolism of snails and the potential significance of lipids to developing schistosomes requires further investigation.

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Aggressive Behavior of the Whelk *Morula musiva*

by

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Introduction

Invasion of one animal's resources by another individual often triggers an aggressive behavior. Among prosobranchs some limpets show aggressive behaviors (STIMSON, 1970; BRANCH, 1979, 1981; IWASAKI, 1992). However, in other prosobranchs aggressive behaviors have not been reported except for the fighting conch *Strombus pugilis*. In the laboratory males of this species fight for their mates using the proboscis (BRADSHAW-HAWKINS & SANDER, 1981). I found in the laboratory that *Morula musiva* (Kiener), a common whelk in the intertidal rocky shore of southwestern Japan, attacks conspecifics with the proboscis. In this report I describe the aggressive behavior of *M. musiva* and discuss the role of this behavior.

Materials and Methods

Individuals of *Morula musiva* were collected from the rocky shore of Shirahama, Japan (33°43'N, 135°21'E) on 28 April 1991, when the male mounting on the shell of the female was often encountered. Twenty-one mounting pairs were collected and each whelk was marked with an oil marker to distinguish the sex. Collected whelks were placed in an aquarium of 35 × 25 × 25 cm. The seawater was aerated and filtered. Some fresh water, less than ca. 1/10 of the water remaining, was occasionally added to keep the salt concentration constant. Whelks were fed living mussels (*Septifer virgatus*). Behaviors of whelks were observed five times a week from 8 May to 26 July 1991 (67 times in total).

Supplemental laboratory observations were made on 17 and 18 July 1992. In these observations a male was put near a mounting pair and behaviors were recorded with a video camera.

Field observations were made on the rocky shore of Shirahama on 2–3 July 1993, where *Morula musiva* was abundant (ca. 12/m²) in tidepools dominated by the mussel *Hormoya mutabilis*. Behaviors of whelks in tidepools were observed for 5 hr during the daytime low tide and for 2 hr during the nighttime low tide.

Results

Aggressive behaviors of *Morula musiva* were observed on 15 occasions in 1991. On 13 occasions, attacks occurred between a mounting male and another male approaching the mounting pair. First, the mounting male lifted the

anterior part of his shell and then elongated his proboscis to seek the rival. These behaviors were induced by the direct contact of the rival with the soft body. The mounting male pressed the tip of proboscis against the rival's body (Figure 1A). The attacked rival usually retracted his body instantly. Although on one occasion the rival quickly went down from the female's shell, in the other cases he counterattacked the mounting male with his proboscis. When both of them elongated the proboscis, they often pushed each other with their proboscides (Figure 1B): repeatedly, one pushed and then the other pushed back. The fights usually terminated when one male dismounted the female's shell, or occasionally, when one male dropped off (Figure 1C, D). The duration of three fights, recorded from onset to termination, was 12, 32, and 48 min.

Of 13 bouts, the mounting male recorded 11 wins, one defeat, and one unknown conclusion. Outcome was not related to the size of males: larger ones won three times, smaller ones six times, and sizes were similar between contestants (size difference <2 mm in shell length) in the other three cases.

In addition to encounters between mounting and rival males, on two occasions aggressive behaviors were observed when a whelk feeding on a mussel was approached by another whelk. The contestants were heterosexual in one case, and homosexual in the other. In both cases they attacked each other in the same manner as when fighting over a mate, and in both cases the original occupant of the mussel won.

Aggressive behaviors were observed twice in the field. In one case, the mounting male was attacked by another male with the proboscis, and dismounted the female's shell without counterattacking. In the second case, two males attacked each other with their proboscides on the shell of a female.

Discussion

Aggressive behaviors of *Morula musiva* were observed in the laboratory and in the field.

Attacking with the proboscis seems to be effective, because the attached whelk retracted his body and occasionally dropped off the female's shell (Figure 1C, D). The radula may have the ability to damage the body of a rival. The whelks elongated and curved the proboscis, the only apparatus the snail can manipulate like an appendage, smoothly to seek the rival. We can easily imagine the divergent usage of the proboscis as a weapon.

Aggressive behaviors mainly occurred when a mounting male was approached by another male. In this conflict between males over a mate, mounting males won most contests even though their rivals usually counterattacked.

Aggressive behaviors also occurred when a whelk feeding on *Septifer virgatus* was approached by another individual, although the frequency was low. This whelk always drills a hole on the prey shell before feeding, and

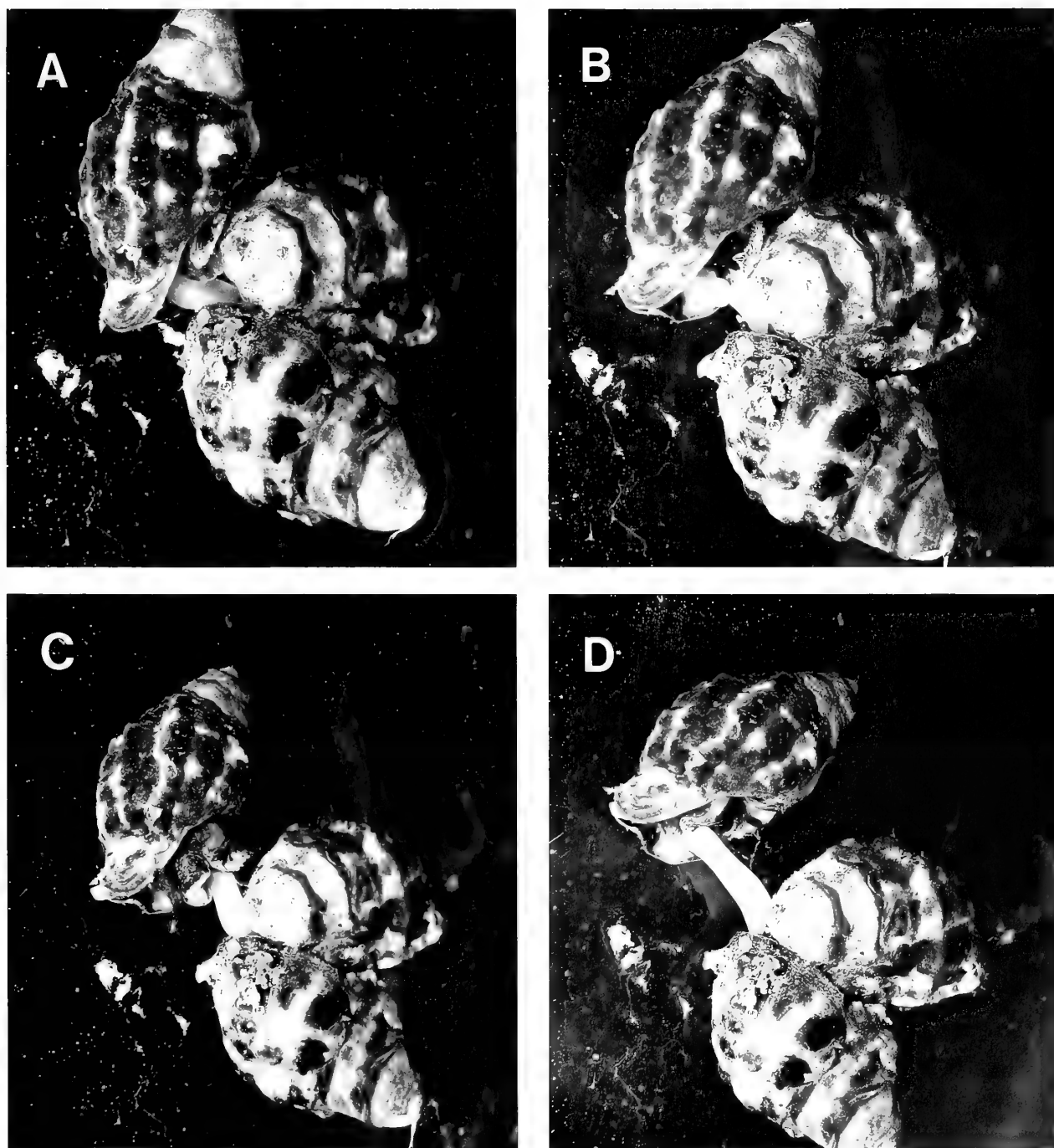


Figure 1

Aggressive behavior of *Morula musiva*. A. A male (lower) mounting a female (middle) and being attacked by the proboscis of a rival male (upper). B. Males pushing each other with the proboscides. C, D. The fight resulted in the drop of the rival male from the female's shell.

drilling takes several hours to three days (ABE, 1989). Thus, the drilled prey is of great value to both the original occupant and a robber. In the field, however, whelks feed only on living animals (ABE, 1980). High density in the

aquarium may cause temporal robbery. In tidepools, scavenging muricids *Ergalatax contractus* and *Cronia margariticola* often gather around the mussel *Hormomya mutabilis* drilled by *Morula musiva* (Abe, unpublished data). Perhaps

the aggressive behavior is important in guarding prey from such scavenging gastropods.

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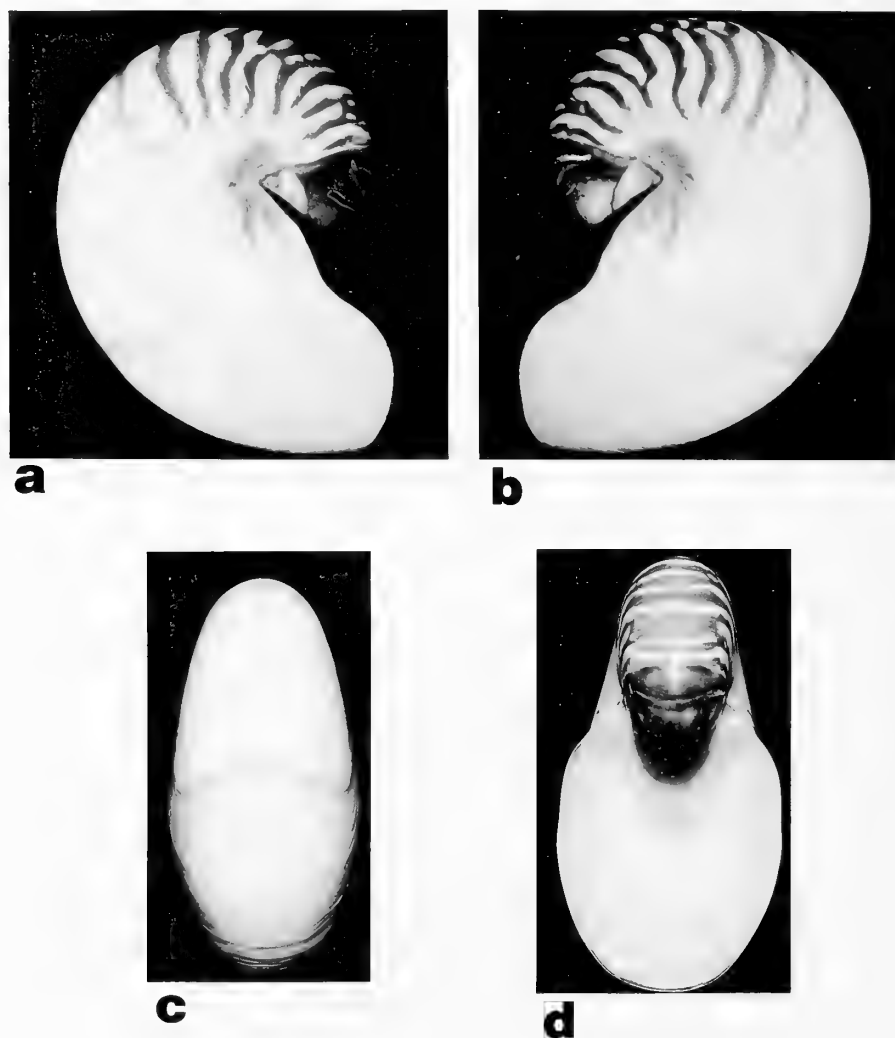


Figure 1

a and b are sides of the *Nautilus pompilius* specimen showing the position of the second band pattern, c shows the second band pattern on the dorsal side of the venter, and d shows the aperture of the shell.

Band Color Pattern on the Venter of a Mature Shell of *Nautilus pompilius* Linnaeus, 1758

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Recently a large shell of the cephalopod species *Nautilus pompilius* Linnaeus, 1758, was obtained with an unusual color pattern. The shell, reportedly from Indonesia, has a diameter of 195 mm, which implies mature size.

Normally, the band color pattern is seen on approximately the first one-third of the mature shell of any species of living *Nautilus*. On this particular specimen of *N. pompilius*, the band color pattern reappears on the white ventral area of the shell (Figure 1a-c). Appearance of the band color pattern on the venter of the mature shell of any species of living *Nautilus* species has never been reported.

There are ten characteristics of the mature *Nautilus* shell (COLLINS & WARD, 1987). Eight of these ten characteristics are detectable through a simple inspection of the shell. Those eight characteristics listed in order of formation by COLLINS & WARD (1987) are:

1. Cessation of secretion of color bands on the shell.
2. Rounded broadening of the aperture.
3. Change in coiling.
4. Contraction of the aperture.
5. Deepening of the ocular sinuses.
6. Full growth of the mature body chamber.
7. Thickening of the apertural edge.
8. Secretion of the black band inside the aperture.

The specimen of *Nautilus pompilius* discussed here has all eight characteristics of shell maturity. (An apertural view of the shell is shown in Figure 1d.) Reasons for the resecretion of the band color pattern in this shell are not clear.

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Range Extension for the Land Snail *Eremarionta rowelli hutsoni*

(G. H. Clapp, 1907)

by

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On 24 March 1992, while performing field research for a status survey sponsored by the U.S. Fish and Wildlife Service, I found two live adult and several shells of *Ere-*

marionta rowelli hutsoni (G. H. Clapp, 1907) in the north end of the Sierra Estrella in Maricopa Co., just southwest of Phoenix, Arizona. These snails were found in rocks lining a north-facing ravine at 112°20.4'W, 33°20.8'N, at an elevation of 393 m. This locality is approximately 187 km east of the nearest previously known locality for *Eremarionta* Pilsbry, 1913. The nearest previously known locality is the type locality for *E. r. hutsoni* and is located in the northern foothills of the Dome Rock Mountains at ca. 114°20'W, 33°35'N, about 6 km west of the town of Quartzsite.

Of the subspecies of *Eremarionta rowelli*, the snails from the Sierra Estrella resemble *E. r. hutsoni* in every important way. PILSBRY (1939) describes *E. r. hutsoni* as being discernible from other subspecies of *Eremarionta rowelli* (W. Newcomb, 1865) by virtue of a broad brown band on the top of its shell. This broad band is separated from the dark brown peripheral band common to *Eremarionta* by a thin white line. The broad brown band extends to the suture, is lighter in color than the peripheral band, and is most obvious when viewed on the inside through the aperture. Below the dark band the shells are light cream colored.

The shells I collected are typical *Eremarionta rowelli hutsoni*. The three adult shells all consisted of 4¼ whorls, their height varied from 8.7 to 9.2 mm, their greatest diameter from 14.5 to 15.5 mm, their peristome height from 7.1 to 7.6 mm, and each shell collected had papillose embryonic whorls common to *Eremarionta* (PILSBRY, 1939).

The reproductive tracts of the two snails that I was able to dissect have typical *Eremarionta* characteristics as enumerated by BEQUAERT & MILLER (1973). These include a dart sac seated on the vagina with two membranous mucous glands attached near its base, and a prominent diverticulum on the spermathecal duct.

The finding of *Eremarionta* in the Phoenix area lends weight to Walter B. Miller's theory that the genus *Sonorella* Pilsbry, 1900, arose through saltational loss of accessory reproductive organs from *Eremarionta* or an ancestor very similar to it (MILLER, 1967; GREGG & MILLER, 1969; BEQUAERT & MILLER, 1973). This is because several members of the genus *Sonorella* in the Phoenix area closely resemble *Eremarionta*. These include *Sonorella rooseveltiana* S. S. Berry, 1917, and *Sonorella allynsmithi* Gregg & Miller, 1969. These snails resemble the *Eremarionta* in their small size, light shell color, nearly black body wall, and their proclivity for the lowest, hottest, and most arid habitats (GREGG & MILLER, 1969).

Acknowledgments

Thanks are due to the U.S. Fish and Wildlife Service, Ecological Services Office in Phoenix, and especially to Sally Stefferud for recommending me for the contract for the study for which this research was a part. I also thank Sally for much patience in helping me with the paperwork involved in this research and for taking time out of her busy schedule to join me in the field a few times. I would

also like to thank my mentor and friend Walter B. Miller, of the Santa Barbara Museum, who was the person I called immediately upon dissecting the first of these snails and finding that it was an *Eremarionta* rather than a *Sonorella* as I had thought. I thank him for much help and guidance on this and many other projects.

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Change in Editorship of *The Veliger*

Farewell and Thank You from the Departing Editor

When I was appointed editor of *The Veliger* in July 1982, some, even some within the California Malacozoological Society (CMS), were not certain the journal could, or should, continue without its founding editor of 25 years, R. Stohler. Eleven years and over 4000 journal pages later we are still serving our mission—to provide a forum for scholarly communication about mollusks.

That we have been able to continue publishing a quality scientific journal is testimony to our readers and to three other groups of people I would like to thank: those who submitted manuscripts for consideration, those who reviewed the manuscripts, and those who transformed the manuscripts and illustrations into a polished, final product. Although the editor serves as a facilitator, the quality and success of a scientific journal rests largely on the quality and abundance of submitted manuscripts, the efforts and skills of its reviewers, and the professionalism of the printing house. Thank you all—readers, authors, reviewers, and Allen Press, Inc.

I feel honored to have been part of the process, and I thank CMS for the opportunity to serve the authors and readers of *The Veliger*. I have been especially pleased and satisfied by opportunities to assist first-time authors, by the growing international and trans-American flavor of

the journal (authors in Volume 36 alone represented 18 countries and 14 states), by the breadth of our reviewer base (over 300 different scientists have contributed their views on manuscripts), and by the consistently high-quality, timely product that the crew at Allen Press, Inc., has put out (each of the 42 issues was published exactly on the date printed on the cover).

The future looks bright. May all of you, and your journal, fare well indeed.

D. W. Phillips

Dr. Barry Roth is New Editor of *The Veliger*

CMS has appointed Dr. Barry Roth as Editor of *The Veliger*, and we are cheered that he has accepted the post. Dr. Roth, the author of numerous scientific publications on land snails and paleontology, is a long-time contributor to *The Veliger*, as an author, a reviewer, and a member of the Board of Directors. We are in capable hands.

Effective immediately, please send all new manuscripts to:

Dr. Barry Roth
Editor, *The Veliger*
745 Cole Street
San Francisco, CA 94117, USA

BOOKS, PERIODICALS & PAMPHLETS

"Larval" and Juvenile Cephalopods: A Manual for Their Identification

edited by M. J. SWEENEY, C. F. E. ROPER, K. M. MANGOLD, M. R. CLARKE & S. V. BOLETZKY. Smithsonian Contributions to Zoology, no. 513, 282 pp.

The ecological and economic importance of cephalopods in marine ecosystems and fisheries is veiled by our ignorance of the group. Adult squids generally evade capture, but young squids, being slower and less maneuverable, are more often caught. These stages of the life cycle, however, have been the most difficult to identify. By summarizing our knowledge of young coleoid cephalopods and providing keys, this manual attempts to make their identification simpler and directly comparable between workers. Information exchanged among 35 international experts during a 1985 workshop forms the basis for this manual. Previously published data and figures of young of all described coleoid cephalopod families are presented by the 31 contributors, who, when possible, add new material. Although juvenile stages are unknown from some families (*e.g.*, Psychroteuthidae, Architeuthidae, Neoteuthidae), these families are included to insure completeness.

A figured guide to cephalopod terminology (including adult characters) begins the volume; a provisional key intended to enable identification of specimens to the family level follows. Although supplemented with an illustrated glossary, this key falls short of its objective. The warning that family identifications are not to be based solely on the key must be heeded. Accurate identifications require reference to taxonomic diagnoses and illustrations in the manual and to additional literature. A table summarizing key characters of each family would have been helpful. I suspect most users will develop their own version of such a table, one that includes page references to the pertinent sections in the manual.

The main objective of this volume is accomplished in the 26 chapters devoted to the families of Oegopsida (open-ocean squids). This volume is the first to provide a nearly comprehensive summary of our knowledge of young squids. Detailed treatments of these families reveal their morphological diversity and often allow identification of genera and, sometimes, species.

The uniform structure of the chapters is a helpful feature of the manual, and especially impressive given the diversity of authors. Brief diagnoses of adults, young, and eggs are followed by a key (or keys) to genus or species level. Both adult and juvenile specimens of each genus are figured and a short list of recommended references is provided. Exceptionally complete and thorough treatments include those for the Enoptoteuthidae, Ctenopterygidae, Histioteuthi-

dae, and Cranchiidae. In these families, a wide size range of specimens is illustrated in directly comparable figures.

That the purpose of this volume, to standardize methods of identifying young cephalopods, is important can be seen by considering the Gonatidae. Much of our knowledge of North Pacific gonatid distribution is based on hatchlings and juveniles (*e.g.*, KUBODERA & JEFFERTS, 1984a, b). By explicitly outlining how species are identified at various stages in development, this publication allows other workers to evaluate these criteria and make comparable determinations.

In contrast to the species-level identification possible among the young of some open-ocean squids, identification of the young from other groups cannot yet be readily accomplished. In a group for which larval identification would be most welcome, the myopsid squids of the Loliginidae, the potential for larval identification appears to be limited. Hatchlings of loliginid species from the well-studied fauna of the west North Atlantic can at best be identified to the level of genus. In other areas, even generic identifications of young are uncertain.

Among the Octopoda, the low species-level diversity of the pelagic and mesopelagic octopods generally allows species-level identification. One quite unexpected inclusion in this identification manual is that among the mesopelagic octopods of the Bolitaenidae: the genus *Dorsopsis* is synonymized with *Japetella*.

Among planktonic young of comparatively shallow-water octopodids, chromatophore patterns, rather than morphological characters, are advocated as the means to identify taxa. Although five of the 17 species figured are indicated to have been "thoroughly studied," this section begins with the caveat that it cannot be used to identify species; rather these 40 pages describe chromatophore organ patterns. Given the little morphological variation in octopodids, chromatophores may assist in their identification; the arrangement of chromatophores and suckers, coupled with sucker number and arm length patterns, have been shown to identify "types" of planktonic octopodids, at least locally (YOUNG *et al.*, 1989). If, instead of illustrating a cross-section of the octopodid larvae of the world, this chapter had addressed octopodids by geographic area, as accomplished in the loliginid treatment, perhaps a measure of certainty could have emerged.

This manual is not free of problems. Most figures have been previously published, consistent with the manual's intent to summarize our current knowledge; unfortunately, because the figures were produced by diverse illustrators, they can be difficult to compare. In some families juveniles at the best known or most distinctive stage of the life cycle (*e.g.*, the rhynchoteuthion larvae of the Ommastrephidae)

are the sole focus of the treatment. More detailed definition of critical characters would have been helpful within individual chapters.

To facilitate production of reprints, each family entry begins on a recto page. Unfortunately, this makes use of the manual awkward; the text often refers to figures on the reverse side of the same page. The figures are inconsistently organized on the page. Figure subdivisions are located where they fit on the page rather than in a predictable pattern. Size indications are generally not included on the figures, where they would be discernible at a glance, but are included in small print in the captions.

The seven-year lag between the workshop and publication of the volume has created a real liability. Because publications later than 1987 are rarely incorporated or cited, the volume was out of date prior to its publication. Regrettably, YOUNG's (1991) major addition to our knowledge of the chiroteuthids and related groups is not even footnoted. As the editors thank the workers who strived for timely publication, apparently the delay in publication was not due to universal negligence.

This volume is a comprehensive summary of research on planktonic cephalopods, current as of 1987. This descriptive guide to larval and juvenile cephalopods will greatly simplify their identification. Although not all specimens of all families can be identified with the help of this

manual, this summary of a scattered literature and explicit definition of key characters in identification will prove very useful, especially for oegopsid squids. By making this information accessible to more scientists and highlighting the need for additional work, I hope this volume will attract new people to cephalopod biology. An influx of new ideas and new approaches to solving old problems is critical if this, or any, field of research is to remain vibrant.

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Janet R. Voigt

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

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Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

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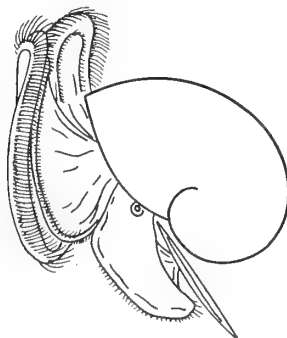
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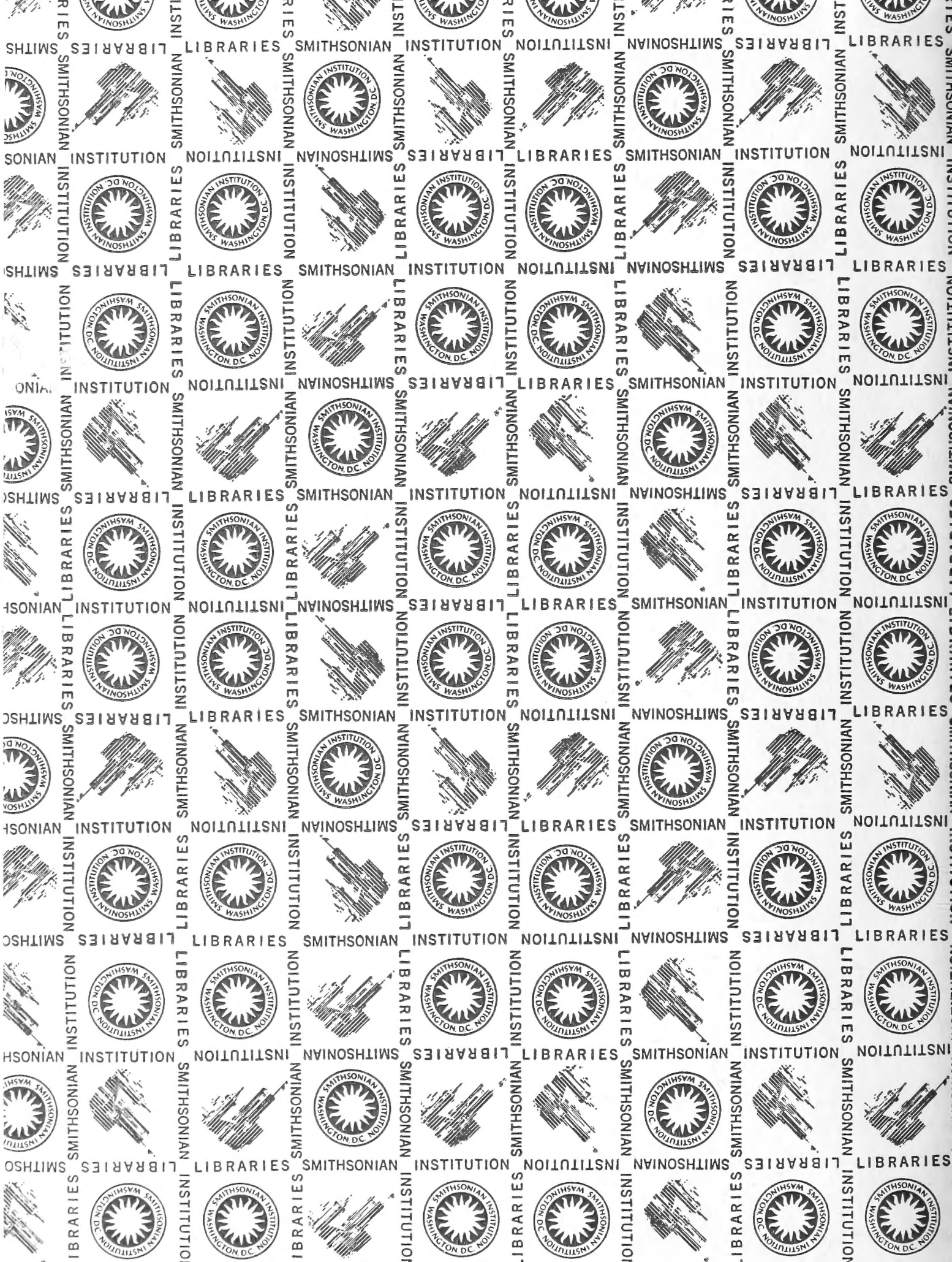
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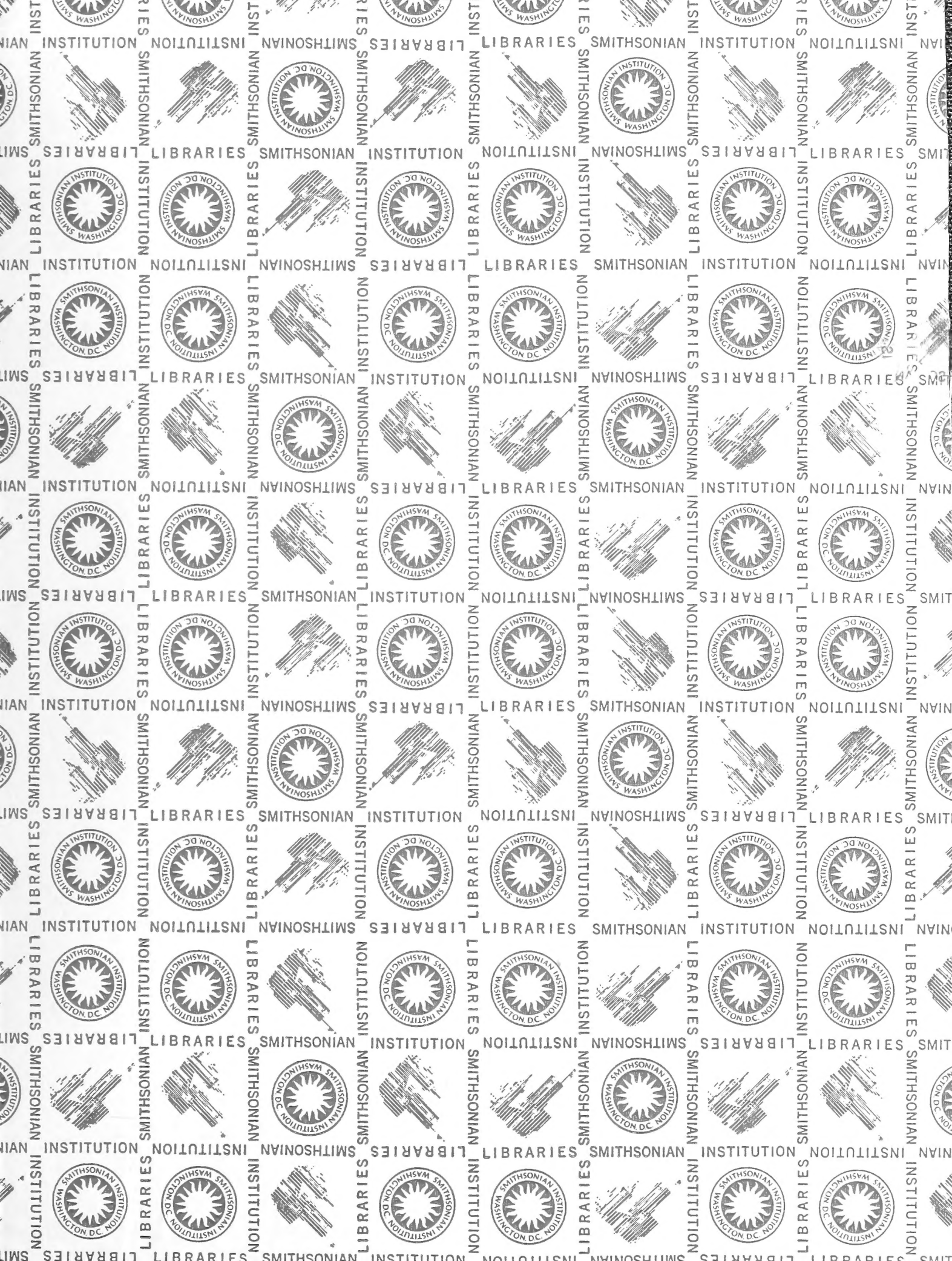
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